GROUND FLORA AND SEED BANKS OF WOODLANDS IN SOUTH WEST ENGLAND

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ABSTRACT

This thesis examines the ground flora and seed banks of a range of forest and woodland types in south west England. Ground flora surveys were carried out and seed banks investigated by sampling and germination trials.

Depletion of both the ground flora and seed banks of conifer plantations and neglected coppice was shown to have occurred after periods of 40-50 years or more. Re-coppicing or clear-felling of such woodlands did not always result in immediate ground flora recovery and subsequent seed bank renewal. After long periods of shade, resulting from neglect or the presence of a dense conifer canopy, the ground flora which develops after felling develops mainly from species which have survived either in the seed bank or in the ground flora. The seeds of many woodland species are poorly represented in the seed bank since they do not survive for long periods in the soil. Since these species are also intolerant of dense shade and they are generally lost from neglected and coniferised woodland.

The diversity of the ground flora and hence the seed bank was shown to be limited by site fertility and fewer species were present at sites with acid soils than at those with more base-rich soils.

Uneven-aged forestry systems were shown to promote a greater ground flora and seed bank diversity than the even-aged, clear-fell system currently used in most British forests. These alternative systems are particularly appropriate for use in lowland Britain. With declining agricultural profitability, recent changes in forestry policy encourage the expansion of forestry on surplus agricultural land. Since soil fertility is generally high on such land, the introduction of alternative forestry systems could fulfil a dual objective of commercially viable timber production with increased ground flora diversity and hence ecological interest.

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CHAPTER ONE : AN INTRODUCTION TO THE THESIS

1.1. INTRODUCTION AND AIMS

Woodland seed banks have been relatively under-researched in comparison with those of arable fields and grasslands (Leck et al., 1989). The few studies which have been carried out in British woodlands have investigated the seed banks of neglected coppice and upland conifer plantations. The seed banks of coniferised lowland woodlands have received little attention. A primary aim of this thesis is to examine the seed banks and ground flora associated with neglected and coniferised coppice woods in lowland south west England.

A further aim of the thesis is to assess the potential of alternative coniferous forestry systems for conserving a diverse ground flora in comparison with the impoverished ground flora generally associated with clear-fell systems. These alternative systems are particularly appropriate for use in areas of lowland Britain where new grants are available for establishing woodlands on surplus agricultural land.

The extent of ancient broadleaved woodland in Britain has declined drastically since 1945 and much coniferisation has occurred (Peterken & Harding, 1975; Peterken, 1976). Current forestry policies and incentives such as the Farm Woodland and Set-Aside Schemes encourage the expansion of forestry in lowland regions; much of this is likely to be coniferous, despite government incentives which encourage the planting of broadleaves.

While many ecologists would be inclined to write off planted coniferous woods as having little potential ecological interest, the possibility exists of increasing ground flora diversity in commercially managed forests. With the traditional coppice and coppice-with-standards systems, a diverse ground flora and seed bank was maintained largely as a byproduct of management practices (Peterken, 1983). The modern clear-fell forestry system is quite unlike the traditional systems. The intensive management methods adopted in order to increase timber production have brought forestry into conflict with nature conservation (Peterken, 1981). A familiar feature of the clear-fell system is the virtual elimination of the ground flora under developing coniferous stands. This thesis attempts to consider ways in which forestry management systems can be changed to encourage a greater ground flora diversity and ecological interest.

1.1.1. More Detailed Objectives

Within the aims outlined above, this thesis sets out to:

a. Study the species composition of seed banks and ground flora associated with different woodland types.

b. Examine the ground flora diversity associated with different silvicultural systems and to identify any changes associated with changes in forestry management practices.

c. Study the longevity and viability of woodland seed banks by comparing the seed banks of areas where changes in forest management have occurred; for example, where conifer plantations have replaced coppice, where uneven-aged stands have been created in place of even-aged plantations and where coppicing has been resumed after many years of neglect.

d. Examine the distribution of seeds in woodland seed banks.

e. Assess the difficulties of sampling seed banks in woodlands with a view to devising improved sampling techniques.

f. Formulate guidelines for encouraging a more diverse woodland ground flora and for revitalising depleted seed banks within coniferous woodlands and neglected coppice.

1.2. STRUCTURE OF THE THESIS

A pilot study was carried out at the Tavistock Woodlands Estate in Devon, where Bradford Plan, an alternative coniferous forestry system, has been introduced. This study provided preliminary information on the ground flora and seed banks under such forests and allowed methods for studying seed banks to be developed. This pilot study is described in chapter two. In chapter three, the methodologies of seed bank sampling and ground flora surveys are reviewed; the sites studied and the sampling and survey procedures used in the project are described.

The main programme of sampling was carried out at a range of sites in south west England. These included a number of even-aged conifer plantations, at Buckley Wood in Devon, the Werrington Park Estate in Cornwall and the Longleat Estate in Wiltshire. Further sampling was carried out of the uneven-aged Bradford Plan units at the Tavistock Woodlands Estate and of an uneven-aged stand of conifers on the Longleat Estate. Abandoned coppice was sampled at Yarner Wood in Devon and at several of the other sites. The results of the ground flora and seed bank surveys are presented in chapters four and five. Within and between site differences in the seed banks and ground floras are discussed in chapter six. In chapter seven, an investigation of the resistance of seeds of a number of woodland ground flora species to fungal attack is described. This was chosen as a topic for study since fungal attack is one factor responsible for seed decay, affecting the longevity of seeds in the seed bank. Finally, chapter eight considers the extent to which the aims and objectives described above have been fulfilled. This final chapter also provides a discussion of the key results of the project and outlines suggestions for further work.

In order to set the thesis in context, the remainder of this introductory chapter examines British forestry policies; various forestry systems are described and their suitability for use in the British lowlands is considered. The general literature concerning seed banks is reviewed, as well as that relating to woodland seed banks and ground flora.

1.3. BRITISH FORESTRY POLICIES

The present woodland landscape of Britain has been influenced greatly by British forestry policies. The following section provides a brief outline of these policies.

1.3.1. Forestry Policies: Historical Perspective

The Forestry Commission was established in 1919, as a response to the realisation during the first world war that Britain was critically short of a strategic timber reserve (Nature Conservancy Council, 1986). Its original role was to act as the State Forestry Authority, to manage existing woodlands and to create new forests so that Britain could be self-sufficient in timber in the event of another war. The foresters at the time were greatly influenced by the German tradition of plantation forestry and its reliance on fast-growing conifers which could realise quicker profits than slow-growing broadleaves. Thus the process of coniferisation began.

State expenditure on afforestation was complemented by encouraging private investment through grant-aid and tax incentives. In 1978, the Forestry Commission planted almost 70% of Britain's trees. However, since 1981 it has been government policy that most new afforestation should be carried out by the private sector. By 1988, private investors were responsible for 80% of all planting. The main reason for this substantial increase of private sector investment in forestry was the exploitation of a tax avoidance opportunity (Miller, 1981; Stewart, 1985) which involved switching between two different tax schedules, Schedule D and Schedule B. Under Schedule B, the costs of establishing and maintaining a plantation were not eligible for tax relief, but the profits from the sale of the timber were almost tax free. This concession was introduced to allow for the long period of time between planting and felling. Under Schedule D, the investor was eligible for tax relief on the expenditure entailed in establishing and maintaining a plantation but any income from the sale of the timber was liable for tax. To take advantage of both schedules, a change in ownership of the plantation was necessary. A typical sequence of events would have been as follows: an investor would establish a plantation under Tax Schedule D, then sell it usually after about ten years, to an individual who would elect to be taxed under Schedule B. The sale of growing trees was exempt from Capital Gains Tax, another inducement to the Schedule D investor. Interest payments on forestry loans taken out to buy the land also qualified for tax relief and planting grants were a further incentive. The Schedule D investor, who claimed all available grants and tax reliefs, could make a return of up to 33.5% per year. Forestry was therefore a very sound investment for high tax payers. Pop-stars, sports celebrities and businessmen are amongst those who have benefitted from the practice, which has resulted in the large-scale afforestation of land unsuited to growing trees and has been condemned by most of Britain's conservation bodies.

In order to avoid competition with agriculture, state afforestation has mostly been restricted to soils of low fertility such as low grade hill sheep pasture, sandy lowland heaths and wet peat bogs. Since large tracts of such poor land exist in upland Britain, large-scale afforestation has been mainly concentrated in upland regions. The Forestry Commission has been able to purchase land suitable for planting at relatively low cost. Cheap land has also been attractive to private investors, since land purchase was the only expenditure which could not be set against tax.

Besides the investors themselves, the forestry companies have also made large profits from afforestation. They act as agents, buying and selling land and establishing plantations. The presence of the state and private forestry companies in the market for hill farmland has caused increased land prices which has brought forestry into conflict with hill farming.

Public money is not normally invested unless it can achieve a rate of return of at least 5% per year. In 1972, the Forestry Commission was set a reduced target of only 3%. Between 1977 and 1982 it failed to meet even this lower rate. New planting is expected to achieve an average return of 2.25% per year, but planting in the north of Scotland is expected to yield only 1.25%. In areas of high windthrow risk, such as the exposed peatlands of Caithness and Sutherland, a combination of poor growth rates and early felling could reduce returns to as little as 0.5% per year (R.S.P.B., 1987). Private forestry can expect to achieve much the same rates of return.

As early as 1980, a report by the Public Accounts Committee (House of Commons, 1980) called for legislation to end the favourable tax system, but nothing was done. In 1986 an investigation by the National Audit Office (National Audit Office, 1986) concluded that incentives for private planting could not be justified. However, it was not until 1988 that changes were made. Under the new legislation, expenses incurred in establishing and maintaining plantations are no longer tax-deductible. Profits from timber sales are now tax-free but in practice, with the opportunity to switch tax schedules, this has always been the case.

British forestry policy has been based largely on the Forestry Act of 1919. Although there have been changes in the target rate of planting and in the involvement of the private sector, the essential element has remained the establishment of state-financed conifer plantations (Stewart, 1985). The justifications given for the policy have changed over the years (Miller, 1981). The initial "strategic" argument (to create a reserve of standing timber in case of future conflicts) was weakened with the realisation in the 1950's that any future wars would be of short duration. Another justification which has been used in support of forestry is the creation of jobs in rural areas. Forestry provides more jobs than the farming it generally replaces, but the work is irregular and if town-based contract workers are employed, the rural communities do not benefit. Forestry jobs are also expensive to create; the National Audit Office has estimated that forestry jobs in the north of Scotland cost twice as much as agricultural jobs. Since Britain imports most of its timber, it has been suggested that it is in the national interest to grow more timber to reduce dependence on imported timber (R.S.P.B., 1987). However, this import-saving argument cannot be supported economically since it costs more to grow the wood than to import it (Forestry Commission, 1979).

1.3.2. Conservation and Forestry

The initial policies of the Forestry Commission were aimed at increasing timber production and were not concerned with conservation, recreation or amenity (Peterken, 1983). Gradually the Commission became more sensitive to public opinion and efforts were made to provide facilities for visitors to forests such as car parks, picnic areas and forest walks. Increasingly, landscape considerations were taken into account when establishing new plantations (Crowe, 1978). However, it is unlikely that the extensive afforested areas in the north of Scotland will ever be used for recreation on a large scale since they are too remote; there are many more convenient plantations further south. People currently visiting these areas do so to appreciate their wildness, natural beauty and wildlife. Upland forests are radically different from the open ground systems they replace. Although they attract their own wildlife, they cannot compensate for the loss of heaths, grasslands and peat bogs which are of high environmental value in their existing states.

Native broadleaved species are too slow growing and/or inferior in timber quality to be acceptable for economic afforestation. Most planting has been with fast-growing introduced conifers mainly sitka spruce (*Picea sitchensis*), Japanese larch (*Larix leptolepis*) or hybrid larch (*Larix* x *eurolepis*) and lodgepole pine (*Pinus contorta*). The restricted choice of species is to some extent reinforced by market demand, the commonly planted sitka spruce finding a ready market as a first class pulpwood.

Conifers can cause soil deterioration (Miles, 1978). Conifer litter is slow to decompose and tends to accumulate as a thick layer on the soil surface; mineral nutrients are immobilised. At sites where conifers have replaced broadleaves, soil acidity increases because conifer litter and decomposition products are more acid. On poor soils, mor humus accumulates and there is an accelerated rate of podzolisation. Soil fertility can be restored by fertilizing. Soil deterioration is less in some mixed species stands, for example pine with spruce (Brown, 1986) because the release of nitrogen and phosphorus from the litter and soil organic matter is greater in these stands. Conifers elevate the levels of water acidity in forest streams, mainly because evergreen foliage traps acidic aerosol particles efficiently (Harriman & Morrison, 1982). High levels of acidity are harmful to fish. The use of synthetic organic insecticides in forests has been widespread, resulting in their introduction to areas previously free of harmful chemicals. Herbicides are also used to control weed growth, mostly on lowland sites

(Nature Conservancy Council, 1986). The application of fertilizers leads to raised levels of nutrients such as calcium and phosphorus in drainage water (Binns, 1979). This can cause eutrophication effects such as algal blooms in lakes fed by streams from afforested catchments (Gibson, 1976; Harriman, 1978).

It can be argued that reforestation of the British uplands is simply restoring the natural tree cover of the boreal coniferous zone which would have been present if Britain had retained it's land link with the continent (Stewart, 1985). However natural forests, such as those of southern Scandinavia, are generally not pure conifers since broadleaves such as birches and alders are also present. These mixed forests generally provide a good habitat for wildlife.

The main objective of forestry management methods adopted in Britain has been timber production. Operations are mechanised and large-scale, to keep costs low. The growing of monocultures, particularly of introduced species, increases the risk of epidemic pest outbreaks. This is illustrated (Watt, 1986) by the severe damage caused to plantations of lodgepole pine (*Pinus contorta*) in northern Scotland by the native pine beauty moth (*Panolis flammea*), a species which rarely causes significant damage to its native host, the Scots pine (*Pinus sylvestris*). The risks associated with growing monocultures of exotic species are accepted since the potential gains in production more than compensate. The introduction of silvicultural methods which reduce the risk of pest outbreaks would, however, make ecological sense.

The homogeneous even-aged stands of modern conifer plantations are the least attractive form of woodland for wildlife and habitat conservation (Peterken, 1981;

Peterken & Harding, 1983). Plantations which reach maturity as well-thinned stands are more diverse than the young closed canopy stages but in many plantations, particularly where windthrow hazard exists, early felling precludes the development of mature well-thinned stands.

The selection forestry systems commonly used in mountainous regions of Europe aim to treat the forest as a community of indigenous species, creating stability by emulating natural conditions as closely as possible. In Britain, it would be difficult to create commercially viable selection forests.. However, alternative forestry management systems suitable for use in lowland Britain have been developed, such as the Bradford Plan system at the Tavistock Woodlands Estate in Devon. This system is described in detail later in this chapter (section 1.4.1.).

In a recent report, Gamlin (1988) has discussed the environmental problems created in Sweden as a result of the intensification of forestry methods aimed at increasing timber production. Forestry is important to the Swedish economy, which is based on the export of wood products, mainly pulp and paper. The use of fertilizers has been encouraged and fast-growing exotic species, such as *Pinus contorta*, have replaced native conifers (*Pinus sylvestris* and *Picea abies*). Wetlands have been drained and native mixed forests felled and replanted with conifers. There has been a trend towards large-scale clear-felling and increasing mechanisation. Many forest species have declined as a result of these changes and long-established forests are being felled at an increasing rate. Following criticism by environmentalists, some forestry companies have returned to felling smaller areas but small-scale felling is often uneconomic. In contrast, selective felling has been employed successfully in some parts of Finland where a less intensive, more conservation-conscious approach to forestry has been adopted.

In Britain, timber production is no longer the only objective of forestry management. Since the Wildlife and Countryside (Amendment) Act 1985, the Forestry Commission has had a statutory responsibility to achieve high standards of nature conservation in forestry. Conservation guidelines (Forestry Commission, 1990) have been published to provide guidance on the maintenance and enhancement of the nature conservation value of existing woodlands and on taking opportunities to develop nature conservation in new planting.

With increasing standards of living, more leisure time and improved transport facilities, there is a demand for forests, especially those near large towns, to be managed for recreation and amenity. The Countryside Commission and the Forestry Commission (Countryside Commission, 1987a, 1989a, b) have recently launched a Community Forest initiative, proposing the creation of urban fringe forests as well as the establishment of a new forest in the English Midlands.

Few ancient broadleaved forests remain in Britain. One exception is Epping Forest, on the northern edge of London. This surviving remnant of the great Forest of Essex provides a major tourism and recreation resource as well as being of high amenity and conservation value. The new Community Forests, whilst not aiming instantly to re-create ancient broadleaved woodland, will provide opportunities for leisure, sport and nature conservation as well as timber production and the development of economic enterprises based on forestry and tourism. Other European countries have already created recreational urban fringe forests, such as the 40 year-old Bos Park on the outskirts of Amsterdam. In Germany there are many of these forests, called Stadtwalder (town forests) which were created over 200 years ago, on land with low potential for urban or agricultural use (Countryside Commission, 1989b).

Conservation imposes costs (Lorrain-Smith, 1973, 1991). Many forestry practices which are hostile to wildlife have been adopted because they reduce costs. The full benefit of mechanisation, for example, can only be realised if operations are large scale. This conflicts with the small-scale working required to produce diversity within forests. The loss of potentially productive land which occurs, for example if rides are widened and wet areas retained, must also be counted as a cost. Most native trees are slower growing than exotic species, which results in a delayed return on investments, making them worth less.

Despite increased costs, there are a number of benefits that might result from expenditure on conservation. Conservation may be profitable in a direct way, through the sale of timber and other forest products, or through the sale of sporting licences for hunting and shooting. Less obvious benefits may result from the preservation of a natural system, such as biological control and the maintenance of soil fertility. Other social benefits include the use of the forest for recreation, amenity, landscape and research. Not all benefits can be financially exploited. The intuitive feeling that wildlife is worth conserving may be due to a sense of responsibility to protect living things irrespective of their material worth or of the possible dangers of not doing so.

1.3.3. Upland and Lowland Forestry: Future Trends

Upland forestry offers little prospect for change which will increase the conservation value of plantations. Most Forestry Commission plantations continue to be coniferous and in the uplands since it cannot acquire land on better sites (Stewart, 1985).

From about 1930 to 1950, agricultural land in the lowlands could be acquired cheaply and many fields were afforested. Some of the earliest Forestry Commission plantations were established on the East Anglian heaths. During this period many former coppicewoods in the lowlands were replanted with conifers and the total area of woodland extended by conifer planting. As a result, most lowland afforestation has been concentrated in relatively well-wooded areas. In predominantly agricultural areas, less planting has been carried out but clearance on a relatively large scale has resulted in the increasing isolation of surviving woods. The loss of the coppice tradition has resulted in neglect of those woods which remain, except in areas where there has been an active conservation interest (Peterken & Harding, 1975). It is these coniferised and neglected coppice woodlands which are the focus of this study.

In recent years there has been an increasing awareness of the contribution which ancient broadleaved woodland makes to the landscape of lowland Britain. These woodlands are appreciated for their beauty, their importance as wildlife habitats and as historical landscape features (Rackham, 1976, 1980; Peterken, 1981). The extent, distribution, composition and management of British woodlands has changed over the last 40 years. There has been a shift from coppice to high forest, from broadleaves to conifers and from native species to exotics (Peterken, 1976). Although the total area of woodland has increased since 1949, the area of ancient woodland has diminished appreciably (Peterken, 1976; Watkins, 1986). The bulk of the loss has resulted from coniferisation, although losses to agriculture have also been substantial.

The damage to trees in southern England caused by the great storm of 1987 was extensive. This particularly affected privately owned broadleaved woodland and was most severe in mature and over-mature woodlands. It has been recognised (Grayson, 1989) that a wider range of ages in the growing stock would have reduced the scale of the damage. Timber production is often a minor objective in woods in the south of England, which have been managed traditionally for sporting purposes. As a result, trees are often retained past maturity. Earlier felling would lead to losses for the landscape, for recreation and conservation but this must be balanced against the increased vulnerability of over-mature trees to damage and decay. Provided there is an intention to replant, woodland owners should be encouraged to fell marketable timber as this represents sound woodland management practice. In replanting, conifers are often preferred to broadleaves. Again, an important aim of this thesis is to examine the effects on the woodland ground flora and seed banks of conifer planting in lowland woods.

Recent government policy (Forestry Commission, 1985; 1988c) has been to encourage the planting of broadleaved woods in lowland Britain and to ensure that existing broadleaved woodland is not replaced by conifers or cleared for agriculture. However, since no grant-aid or tax incentives are available, many land-owners have found that it is not profitable to manage existing broadleaved woodland under the new legislation. This may result in further neglect of ancient woodlands, unless management is undertaken by conservation groups or by organisations such as the Woodland Trust. In response to the storm damage, supplements to the Forestry Commission's normal planting grants have been made available for replanting damaged woodlands (Grayson, 1989).

Throughout the 1970's, agricultural practices became more intensive, with increased mechanisation and greater specialisation. Policy and market conditions favoured intensive cereal production especially. With declines in agricultural profitability, policies have changed during the 1980's and various incentives have been offered to farmers which aim to reduce surplus agricultural production (Harvey & Bell, 1990). For example, the Farm Woodland Scheme (Forestry Commission, 1988a, b; M.A.F.F., 1988) encourages the planting of trees on productive agricultural land. This scheme entitles farmers to annual payments for land being taken out of agriculture and converted to woodland, in addition to the grants available under the existing Woodland Grant Scheme (Forestry Commission, 1988c).

Another incentive is Set-Aside, a European Commission scheme (M.A.F.F., 1989) which is available for farmers who voluntarily reduce their crop-producing land by at least 20%; grants for tree planting on set-aside land are available through the Forestry Commission and the Woodland Grant Scheme. The intention is to encourage worthwhile investment in timber-growing on farms, to support farm income and rural employment and to reduce agricultural surpluses. However, since growing trees is not a very profitable occupation in the short term, it is likely that most farmers will not participate in the scheme at present compensation and cereal price levels (Countryside Commission, 1987b; Harvey & Bell, 1990).

Unlike the rest of Europe, where farming and forestry are more integrated, Britain has no tradition of farm forestry. Existing farm woodlands are often unmanaged and therefore produce only poor quality timber. Many farmers view forestry as a commercial activity which conflicts with a concern for the landscape and for wildlife. They also assume that farm woodland managed with conservation in mind cannot be profitable. Farmers must be made aware of the potential for producing high quality timber on farm woodlands. Since many farmers lack a knowledge of woodland management there is a need for information-sharing initiatives such as Small Woods Projects, co-operative organisations which aim to promote more effective management of small woods and provide marketing advice (Countryside Commission, 1985).

The extent to which incentives such as the Farm Woodland and Set-Aside schemes will be taken up is uncertain (Harvey & Bell, 1990). The reasons for the introduction of these schemes are primarily economic but the expansion of forestry in the lowlands does provide opportunities to enhance the landscape, promote nature conservation and increase opportunities for recreation and access. In upland areas and on less fertile sites conifers give better returns than broadleaves. On sheltered, fertile lowland sites a much wider range of species can give acceptable returns and high quality broadleaved timber can only be produced from such sites. The prospects for an integrated approach to conservation and forestry are therefore much better in lowland than in upland regions. Alternative lowland forestry management systems are particularly appropriate where timber production combined with amenity is desired in small woodlands.

1.4. SILVICULTURAL SYSTEMS

The new incentives for woodland planting on land currently in agricultural production have been discussed in the previous section. The possibility exists for the wider use of alternative lowland forestry management systems in Britain, with associated benefits for nature conservation. The following section provides descriptions of a number of forestry management systems, ranging from the ubiquitous clear-fell plantation system to the rarely practised selection system. Traditional woodland management methods of coppice and coppice-with-standards are also described.

Pryor & Savill (1986) have discussed three ways in which silvicultural systems differ. These are, firstly, the method of regeneration, for example, coppice, planting, direct seeding or natural regeneration. Coppice systems are clearly distinguishable but most other systems can use any of the other methods. Secondly, the age structure of the stand, which would place selection systems at one extreme and clear-fell and coppice systems at the other. Thirdly, the size of the silvicultural unit, ranging from the compartment of the clear-fell and shelterwood systems, to the groups of the group systems to the individual tree of the selection system. In practice, silvicultural systems may be difficult to classify since one system grades into the next.

1.4.1. High Forest Systems

The clear-fell system

British forestry is based on even-aged plantation high forest managed using the clear-fell system. This form of management, applied to monocultures of fast-growing conifers, produces the most timber at the greatest profit, at least in the short-term (Peterken, 1981). A stand is cleared in a single felling and replaced by an even-aged stand, usually by planting, although natural regeneration can be used. Planting is costly, but avoids the unpredictability of natural regeneration. Stocking is usually much lower than with good natural regeneration, which may result in a crop of lower quality.

The main advantages arise from the simplicity and uniformity of the system, in particular, the ease of felling and extraction. However, there are also disadvantages; these include lack of protection for the young trees during the bare-ground phase, the increased likelihood of soil erosion and the need to control weed and scrub growth during the initial stages before the young trees become established. Plantations have an artificial and uniform species composition and an unnaturally even age-structure. There is also a lack of continuity of forest cover and a sudden change from mature forest to bare-ground when the crop is clear-felled.

The cycle from planting to felling is generally referred to as the rotation. The rotation time can be as short as 35-40 years for some conifers and as long as 120-150 years for some broadleaves. The main costs (site preparation, planting, fertilizing and control of weed and scrub growth) are incurred at the start of the rotation. There may be some income from thinnings, but significant benefits accrue only at the end of the rotation. Economic considerations therefore favour shorter rotations and fast-growing, mainly coniferous, species.

The shelterwood system

This system is commonly used in the oak and beech forests of France. A stand is cleared in two or more successive "regeneration" fellings. The new stand is established in the shelter of the trees remaining from the previous felling, normally by natural regeneration. These are removed in the final felling as soon as establishment is complete. The stands are even-aged, but a two-aged structure is created during the regeneration phase. This phase normally takes 5-20 years, or longer if good seed years are infrequent. Compared with the clear-fell system, there are a number of advantages, for example the costs of planting are avoided, young trees are protected from frost, drought and winds, and soil erosion is less likely to occur. Felling of the previous crop overlaps the establishment of the next crop. Since felling of the mature stand is the most drastic change involved in forestry management, extending the time period over which this change occurs favours both landscape and conservation. However, a major disadvantage is that shelterwood systems require more management skill than clear-fell systems, and the final felling of the previous stand damages the young trees of the new stand.

The shelterwood system has not been used extensively in Britain, mainly because of the low frequency of good seed years and the lack of appropriate forestry management skills. Also, the system can only be used where a mature high-forest stand already exists. In Britain, virtually the only form of shelterwood has been the planting of beech or conifers beneath the shelter of abandoned coppice. It is possible that the system may have been more widely applied if taxation and forestry grants were not based on the use of clear-fell plantation management (Peterken, 1981).

The selection system

Early selection methods began with the haphazard felling of the best trees but this soon caused deterioration of the forests and as a result was no longer practised. Modern selection methods bear little resemblance to earlier methods based on primitive exploitative felling.

Stands managed on a selection system consist of a mixture of trees of all age classes. Felling and regeneration take place simultaneously throughout the stand, so there is no rotation length or regeneration period. Fellings are carried out at 5-10 year intervals and trees of all sizes are removed, with a view to improving the quality of the stand. Natural regeneration is used, which means that planting costs are avoided. The continuity of forest cover provides protection from soil erosion, wind and snow damage, which is the reason the system is widely used in mountainous regions. The best known and most impressive examples are the mixed silver fir (*Abies alba*) forests of central Europe, particularly in Switzerland and France. Silver fir is a shade-tolerant species which can recover from the long periods (30-40 years) of suppression typical of selection forests.

Selection forests are the closest approximation to natural forests although they are quite unnatural, being the product of sustained and skilled forestry management (Peterken, 1981). They have a multi-storied structure which encourages a diverse flora and fauna and they are visually attractive as well as providing valuable areas for amenity and recreation. The maintenance of continuous cover with sustained yield and reliance on natural regeneration is one of the aims of modern selection systems.

In these respects they are similar to the traditional woodland management systems of coppice and coppice-with-standards which were once widely practised in Britain.

The selection system has not been applied extensively in Britain, one of the reasons being that no British species is as shade-tolerant as the silver fir, making a true multi-storied selection stand difficult to achieve (Pryor & Savill, 1986; Garfitt, 1988). The Chiltern beechwoods have been worked as a form of selection forestry but exploitative fellings have been carried out over the last few centuries. The uneven-aged conifer stand at the Longleat Estate in Wiltshire (Plate 1.1.) provides an example of true selection management. It has been developed from 20-30 year old larch (*Larix spp.*) and Douglas fir (*Pseudotsuga menziesii*) plantations, which were thinned to allow natural regeneration to occur. The establishment and respacing of successive crops of regeneration will take place over ten year periods, with fellings/thinnings of the overstorey at five year intervals. Weed control is necessary but as more age/size classes are established and the canopy becomes more complete, weed growth should be reduced. The Longleat Estate was selected as a study site and this particular stand was included in the survey.

Group systems

Group systems are variants of other silvicultural systems; they involve the application of these systems to small areas, rather than to whole stands. Thus there are group-felling, group shelterwood and group selection systems. The group-felling system involves felling all the trees in a group prior to restocking. The crop within each group is even-aged, but the stand contains groups of a range of ages. The group shelterwood system involves the retention of an overstorey to provide shelter for the

Plate 1.1. Uneven-aged conifer stand at the Longleat Estate in Wiltshire.

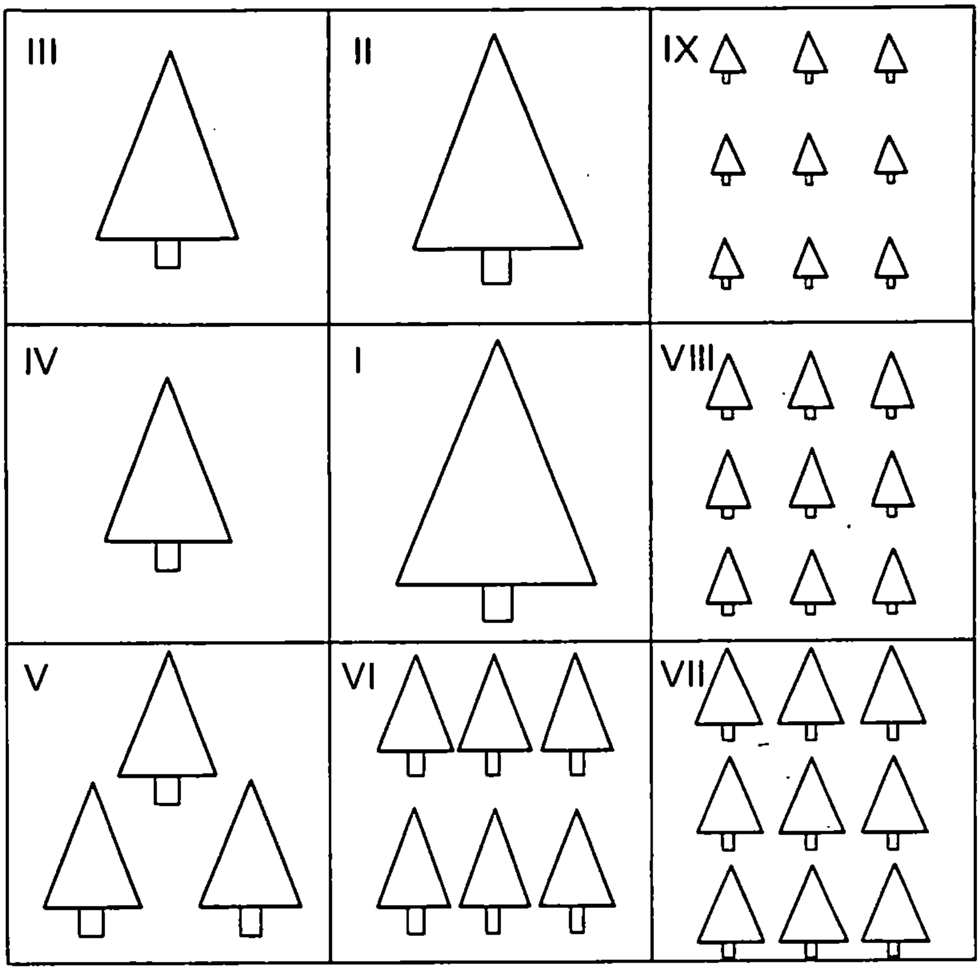
new crop being established in the group, which is approximately even-aged. The regeneration period is longer (15-40 years) than with the shelterwood system, and the crop is therefore more uneven-aged. The group selection system refers to systems in which the stand is sub-divided into groups each of which is for most of the time uneven-aged.

Group systems have been used more frequently in Britain than either shelterwood or selection systems. Group systems are desirable silvicultural systems in terms of landscape, nature conservation and amenity. Group shelterwood and group selection systems are the closest imitation of a natural stand, but the group-felling system produces a structure similar to that of a traditional coppice system. The Bradford Plan (or B-Plan) system, which is being introduced at the Tavistock Woodlands Estate in Devon (Plate 1.2.) provides an example of a group-felling system. However, if the uneven-aged units rather than the even-aged sub-units are considered to be the basic group the system would be classified as a group selection system. The system is of particular interest to this thesis; the Tavistock Woodlands Estate was one of the sites selected for study.

<u>The Bradford Plan (or Bradford-Hutt) system</u>

This system has been described by Hutt & Watkins (1971) and Hutt (1975). The basic group is an 18 m x 18 m unit (Figure 1.1.), divided into nine 6 m x 6 m sub-units. Within each unit a 54 year (nine stage) rotation is used with management at six year intervals. Starting with the central sub-unit, the existing trees are cleared and nine small trees planted. After six years the adjacent sub-unit is cleared and nine more trees planted, and so on. The sub-units are planted in a spiral fashion, working

Plate 1.2. Bradford Plan unit at Blanchdown Wood, on the Tavistock Woodlands Estate in Devon.



Sub-unit	Age	Number of trees
I	54	1
II	48	1
III	42	1
IV	36	1
V	30	3-4
VI	24	6-7
VII	18	9
VIII	12	9
IX	6	9

Figure 1.1. Schematic diagram of a Bradford Plan (B-Plan) unit at the end of the 54-year rotation.

out from the central sub-unit, in order to make the best possible use of the available light. After 24 years the nine trees are thinned, so that by 36 years only one tree remains, this is the final crop tree for that sub-unit. When the system is complete, one tree is harvested from each successive sub-unit every six years. The units are repeated in strips throughout the wood with a network of rackways between the strips for extraction and management purposes (Figure 1.2.). The proximity of mature trees to young newly planted trees in the system make it suitable only for shade-bearing species. Species which have been used successfully are Douglas fir (*Pseudotsuga menziesii*), Western red cedar (*Thuja plicata*), Western hemlock (*Tsuga heterophylla*), Coast redwood (*Sequoia sempervirens*) and Southern beech (*Nothofagus procera*). Each sub-unit is even-aged, but as sub-units are felled and planted at six year intervals, each unit eventually contains sub-units of all ages.

The optimum time to introduce B-Plan into a clear-fell plantation is at the first thinning, around 18 years old. At the Tavistock Woodlands, the system has been introduced into well-established stands and has failed in some areas due to insufficient light levels in the cleared sub-units. Another reason for failure is damage to young trees by rabbits. B-Plan and other selection systems are more wind firm than even-aged systems, but opening up a mature even-aged canopy can cause wind-throw problems. Once the first three sub-units are established, this hazard is past and the stand achieves the greater wind-firmness characteristic of selection forests.

Since the system was only introduced in the late 1950s and early 1960s, it has not reached the completed stage and no sub-units are beyond 30 years of age (Figure 1.3.). However the system appears to be economically viable and capable of producing a

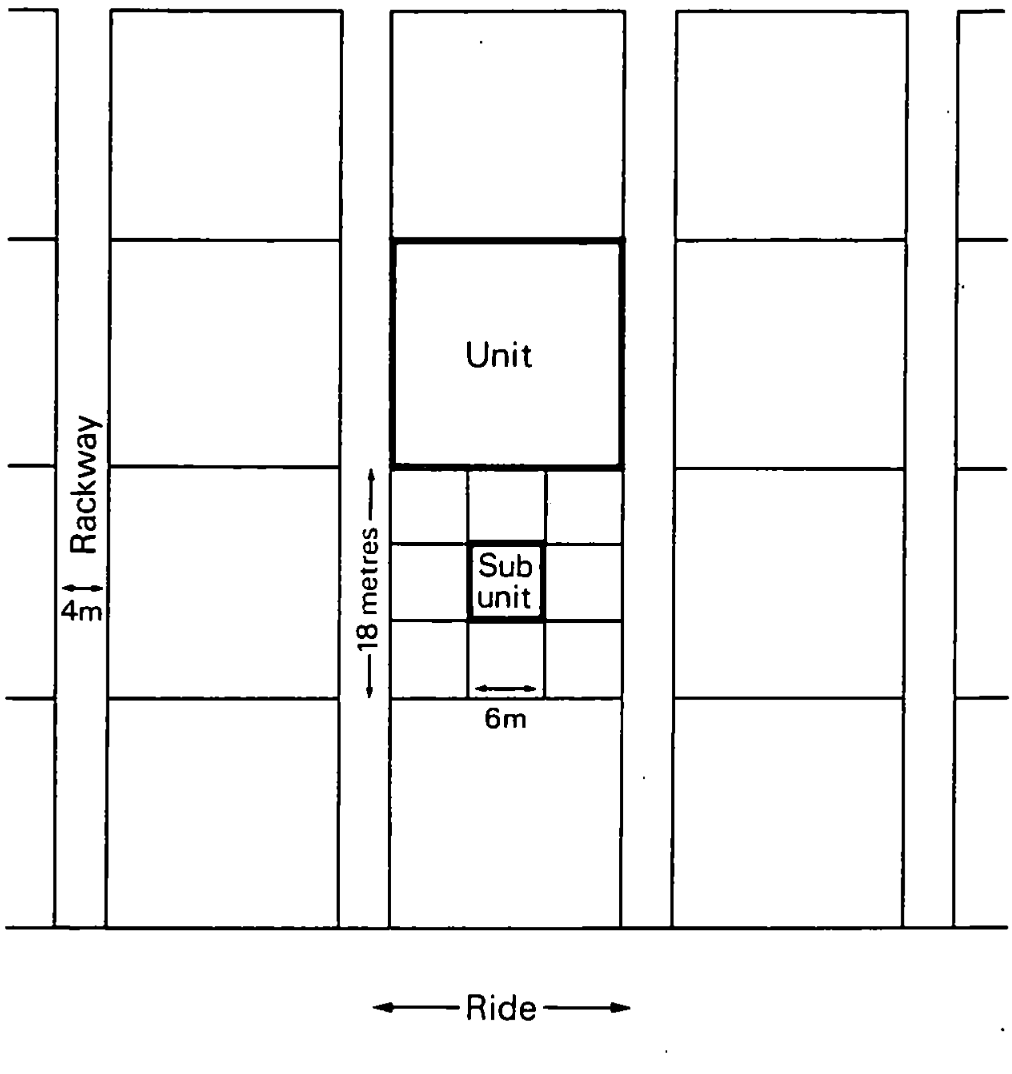
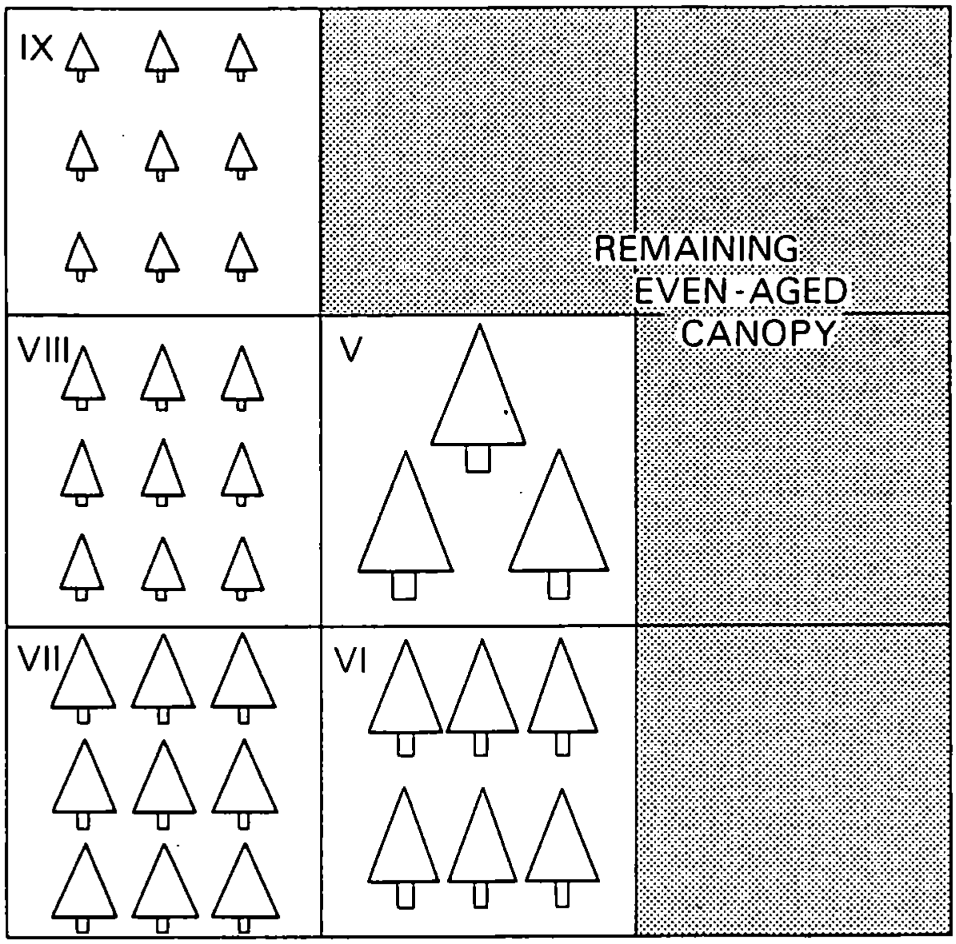


Figure 1.2. Schematic diagram of the Bradford Plan forestry management system, with B-Plan units, sub-units, rackways and ride.



Sub-unit	Age	Number of trees
V	30	3 - 4
VI	24	6 - 7
VII	18	9
VIII	12	9
IX	6	9

Figure 1.3. Schematic diagram of a B-Plan unit midway through the first rotation.

continuous supply of high increment and high quality timber, thus maintaining a steady cash flow and providing employment for a team of trained workers.

The ecological benefits of the B-Plan system are great. The nine stages of B-Plan ranging from cleared ground to mature tree are present within each unit. The open structure and varied tree heights makes the forest more attractive than a conventional even-aged plantation. Light can penetrate to the forest floor during the early stages. The units are replicated throughout forest and the resulting pattern of light and shade allows both the marginal flora (normally associated with the woodland edge) as well as the shade flora (present beneath woodland canopies) to survive. Harris & Kent (1987a, b) have studied various aspects of the system and have shown that species richness in the ground flora in the early stages of B-Plan is similar to the early stages of clear-fell systems. The main advantage of the B-Plan system is that the early stages are replicated and continuously present throughout the wood. B-Plan can take advantage of natural regeneration, as in selection systems. Douglas fir regenerates particularly well in the Tavistock Woodlands and the clearing of sub-units in mature stands stimulates flowering and seed production. The system is flexible, since different species can be planted in the different sub-units, according to market trends. By planting a single species in all the units at any one stage, harvesting and marketing are facilitated, which is why planting is normally used in preference to natural regeneration. Diversity exists within the canopy, since a number of different planted species are present along with native species present through natural regeneration. Hazel (*Corylus avellana)*, rowan (*Sorbus aucuparia)*, birch (*Betula spp.*) and other broadleaves are encouraged as underwood. Light-demanding species can grow in the rides and rackways.

1.4.2. Coppice and Coppice-with-Standards

Coppice and coppice-with-standards is the traditional management of many British woodlands (Rackham, 1980; Peterken, 1981). The word "coppice" derives from the French verb "couper", to cut. The coppice trees and their products are known as "underwood". Part of the wood (a coupe) is cut each year. The stumps of cut trees respond by producing a number of stems; the stumps are called "stools" and crops of poles can be harvested from them at intervals. Coppice woods are broadleaved, since most conifers do not produce coppice shoots. Most native broadleaves can be managed as coppice although some species, including beech (*Fagus sylvatica*), birch (*Betula spp.*) and cherry (*Prunus avium*), do not coppice vigorously (Crowther & Evans, 1984). Periodic cutting actually extends the life of most underwood trees, a coppiced ash stool, for example, may be hundreds of years old. Timber can also be produced from uncoppiced trees (standards) scattered amongst the underwood. Coppicing is a flexible system of management which can be adjusted in response to changing demands for wood and timber. Coppices were formerly an integral part of the agricultural economy, mainly supplying local needs. The underwood was used as firewood and in various craft industries to produce items such as bowls, baskets, hurdles and fencing, while the standards provided timber for building. Underwood (hazel (*Corylus avellana*), ash (*Fraxinus excelsior*), lime (*Tilia spp.*), elm (*Ulmus spp.*) and maple (*Acer campestre*) were valuable coppice species) was cut when it reached marketable size, generally on a 5-30 year rotation. Standards, usually oak (*Quercus spp.*), were felled when they were 25-70 years. New standards were produced by the promotion of a single coppice shoot from a felled standard or by natural regeneration, so planting was not necessary.

Traditional coppice management and plantation forestry co-existed from the 17th to the 20th centuries. Over this period, planting gradually became a feature of coppice management (Peterken & Harding, 1975). The decline in coppice management started in the late 19th century. In 1905, coppice woods were present throughout Britain but by 1945 they were mainly confined to the English lowlands, Welsh Borders and the Lake District. The system had been largely abandoned by 1965, although it was still practised in some parts of south east England. Economic and social factors were responsible for the decline. With the introduction of the railways, mainly between 1840 and 1870, cheap coal became available in country districts reducing the demand for firewood (Rackham, 1976). Also, imported softwoods became a cheaper alternative to home grown timber and as a result coppicing became less profitable. Fewer apprentices were recruited into the coppice crafts as better paid and less arduous work became available in towns and cities. A great deal of timber was felled during the two World Wars and coppicing was largely abandoned as a form of management. To-day, coppice management only survives in a few places where craftsmen still produce traditional coppice products. Examples of worked coppice include Bradfield Woods in Suffolk (Rackham, 1976) and Ham Street Woods in Kent (Peterken, 1981). There has been a recent revival of interest in coppicing due to rising costs of firewood and an increase in the popularity of wood-burning stoves. There is a possibility of new markets developing, for example, the production of corrugated brown paper for packaging requires hardwood pulpwood which can be supplied from coppice. There has been an increase in public awareness of conservation and a number of conservation organisations have attempted to revive coppicing as a woodland management technique (Peterken, 1972; Rackham, 1975).

Coppice and coppice-with-standards are considered to be desirable woodland management methods for nature conservation for a number of reasons. The alternation of the light and shade phases on a short cycle encourages a rich woodland flora. If the annual coupes are small, a good diversity of habitats is produced within the wood, with a continuous gradation from open conditions to closed canopy. When standards are present, they provide a second canopy layer and continuity of woodland conditions. The coppice system can be less desirable if it consists of planted areas of a single species, felled in large coupes. Without the continuity of the standards, coppice can even be less desirable from the landscape point of view than the clear-fell system since the bare-ground phase occurs more frequently than with a high forest rotation. It is also possible that coppicing causes long-term soil degradation because nutrients are lost from the soil during the bare-ground phase and when bark is removed (Pryor & Savill, 1986).

Neglected coppice eventually becomes similar in structure to high forest. Competition and self-thinning take place until the stools support only one or two large trunks. The light phases become infrequent and unpredictable, occurring as a result of treefalls. The diverse ground flora characteristic of managed coppice is then lost. In contrast to the clear-fell system, the alternative (selection and group) systems, described earlier in this section, are similar to the coppice and coppice-with-standards systems in that they have the potential to maintain a diverse ground flora and seed bank.

1.5. SEED BANKS: A Brief Introduction and Literature Review

A principal aim of this thesis is to study seed banks under a range of forest and woodland types. . The following section reviews the existing seed bank literature relevant to the thesis. The subsequent section is concerned with the literature relating specifically to woodland seed banks. Seeds are incorporated into the soil where they form a seed bank. An understanding of the functioning of the seed bank requires a knowledge of its dynamics (Figure 1.4.). Large numbers of seeds may remain dormant but viable in the soil for many years. Several studies have shown that seed banks play an important role in the revegetation of disturbed sites eg. following clearance in tropical forests (Uhl et al., 1981; Young et al., 1987; Lawton & Putz, 1988) and on abandoned fields (Marks & Mohler, 1985). Species represented in the seed bank may have been derived from the current vegetation or from vegetation present at the site in previous years. The ecology of seed banks has been discussed by Harper (1977), Roberts (1981) and Fenner (1985). An extensive recent review of seed bank literature has been provided by Leck et al. (1989).

1.5.1. Species Composition of Seed Banks and Correspondence with Ground Flora

A lack of correspondence between the species present in the seed bank and in the current vegetation has been observed in grasslands (Chippindale & Milton, 1934; Major & Pyott, 1966; Hayashi & Numata, 1971), wetlands (van der Valk & Davis, 1976; Smith & Kadlec, 1983; Wilson, Moore & Keddy (in press)) and in woodlands (Oosting & Humphreys, 1940; Hayashi & Numata, 1964; Petrov, 1977; Brown &

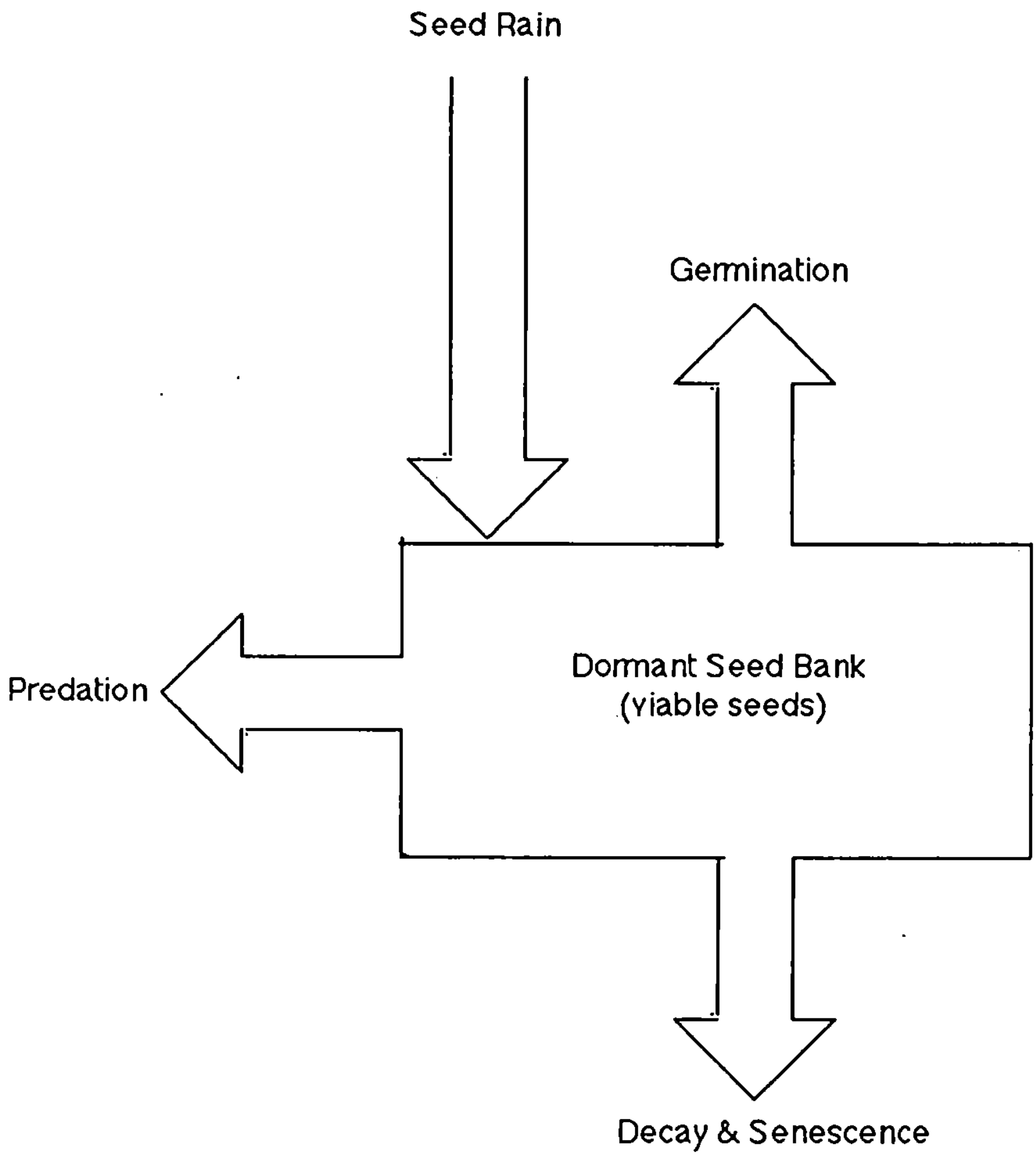


Figure 1.4. Flow diagram for the dynamics of the soil seed bank
(Modified from Fenner, 1985)

Oosterhuis, 1981; Pratt et al., 1984). Thompson & Grime (1979) also found a lack of correspondence between the species composition of the seed bank and that of the associated vegetation in a range of vegetation types in northern England. The lack of similarity between some seed banks and the associated vegetation seems paradoxical since the existing vegetation is likely to be an important source of local seed (Harper, 1977).

In frequently disturbed habitats, the species composition of the seed bank and the vegetation is usually similar, for example in arable fields (Jensen, 1969; Wilson et al., 1985). In undisturbed habitats there is generally less correspondence between the species present in the seed bank and the vegetation. This has been demonstrated in a survey of mature forest soils in Ghana (Hall & Swaine, 1980), in which four out of six sites had a mean of only 5% of their species common to both the seed bank and the vegetation, while in the other two sites none of the species was the same. The effect of disturbance on species composition of the seed bank has been illustrated by Kellman's (1974) study of a 100 year-old conifer forest and an adjacent 7 year-old regrowth stand. For the mature forest site, 16 species were found in the seed bank. Although six (38%) of these were present in the vegetation, only three (19%) were actively contributing to the seed rain. In the regrowth stand, 16 species were recorded in the seed bank; 11 (69%) of these were present in the vegetation and 13 (81%) were collected in the seed rain.

Livingston & Allessio (1968) found that the soil under a climax community contained viable seed of most of the preceding seral stages and concluded that this seed was derived from the vegetation of those stages. Other studies have shown that most of the seed in the soil is derived locally rather than by immigration (eg. Brown & Oosterhuis, 1981; Hill & Stevens, 1981). Some immigration does occur, for example Kellman (1974) found that small quantities of seed could disperse from a regrowth stand into undisturbed forest and become incorporated into the seed bank.

Studies of successional communities have shown that seed bank density, as well as species richness, generally decreases with successional maturity (Oosting & Humphreys, 1940; Livingston & Allessio, 1968; Numata et al., 1964; Nakagoshi, 1984, 1985). Late successional communities, such as undisturbed forests, often have relatively few buried viable seeds (eg. Whipple, 1978), although new seed inputs may occur following opening of gaps in the canopy (Marquis, 1975).

Many of the species which characteristically form seed banks are early successional species, for example the weeds of agricultural soils (Jensen, 1969; Roberts, 1970). Tropical seed banks are similar to temperate ones in being large when disturbance is frequent and in being composed mainly of early successional species (Keay, 1960; Kellman, 1978). One major difference between the seed banks of tropical forests and their temperate counterparts is that tropical forest seed banks consist almost entirely of pioneer tree and shrub species whereas few tree and shrub species are present in those of temperate woodlands.

1.5.2. Seed Longevity and Depth Distribution in the Soil

Little is known about how seeds get into the soil. Oosting & Humphreys (1940) suggested a gradual process in which seeds are buried as a result of litter accumulation and soil forming processes. However, more rapid incorporation of seeds into the soil is likely to occur as a result of freeze-thaw cycles, rainwater percolation and the activities of soil fauna such as earthworms (Harper, 1977; Grant, 1983).

A number of studies have shown that generally there is a depth-related decrease in seed density within the soil profile (eg. Hayashi & Numata, 1964; Kellman, 1970; Moore & Wein, 1977; Kramer & Johnson, 1987). Some species are more abundant near the surface, others in deeper layers, while some show an almost constant distribution with depth (Kellman, 1978; Young, 1985; Young et al., 1987). Litter may contain large numbers of seeds, but in at least one study (Hill & Stevens, 1981) the litter and humus layers were found to contain fewer seeds than the mineral soil.

Deeply buried seed is assumed to be older than seed near the soil surface (Chippindale & Milton, 1934; Moore & Wein, 1977; Kellman, 1978; Hill & Stevens, 1981). Short-lived seed loses its viability before reaching the lower soil layers, so tends to be present only near the soil surface. Long-lived seed may be present in both the upper and lower layers. Kjellsson's (1988) study in Danish forests showed that seeds of species with short-term survival such as *Anemone nemorosa* and *Oxalis acetosella* were confined to the top soil, while seeds of species with long-term survival such as *Carex pilulifera* and *Stellaria media* were found predominantly deeper in the soil. There is some evidence that seed viability is retained longer with increasing depth of burial in the soil (Rampton & Ching, 1970). However, this may be because losses due to predation and germination are less at greater depths in the soil. Darby (1987) studied the distribution of seeds in woodland soils at the Tavistock Woodlands Estate in Devon and found that in undisturbed woodland, seeds were present lower down the soil profile with increasing age. These results illustrate the greater loss of seeds from the upper soil layers and preservation only at depth. Higher losses of seeds in the superficial layers than in the deeper layers has also been reported in agricultural soils (Roberts & Feast, 1972). It appears that larger seeded species decay at faster rates than small ones (Toole & Brown, 1946; Thompson, 1987) although this may be because small seeds are more easily incorporated to greater depths in the soil than larger seeds.

The rate of depletion of buried seed has been studied by artificial methods in which seeds are placed in containers which are recovered at intervals (Toole & Brown, 1946; Darlington & Steinbauer, 1961; Kivilaan & Bandurski 1981) and by observation of naturally occurring seed or seed placed directly in the soil (Roberts, 1962, 1964; Roberts & Dawkins, 1967; Roberts & Feast, 1972, 1973). The former experiments have shown that the longevity of seeds of different species is very variable and that the seeds of some species can retain their viability for periods of at least 100 years.

The causes of depletion of buried seed are germination, predation and loss of viability (Roberts, 1970). This is illustrated by a study (Sarukhan, 1974), in which the fate of buried seeds of three species of buttercup (*Ranunculus*) was followed over a 14 month period. Many seeds were predated by small mammals. Of the seeds remaining different proportions remained viable depending on the species. A large proportion of the seeds of *R. acris* and *R. bulbosus* germinated during the study period and those which did not germinate lost their viability. In contrast, only a small proportion of the seeds of *R. repens* germinated, the others remaining viable in the soil.

Another cause of depletion of buried seed is fungal attack (Roberts, 1970). Since this has never been investigated, the role of fungal attack in seed decay was chosen as a topic for inquiry. A study was undertaken in which seeds of different woodland species were tested for susceptibility to attack by fungi which occur commonly in woodland soils. This study is described in detail in chapter seven.

Soil conditions influence the mortality and longevity of buried seeds (Milton, 1936, 1943). High viable seed numbers often occur in peaty, acid soils (Champness & Morris, 1948; Granstrom, 1988). However this may be because the species associated with such soils, such as *Juncus effusus* and *Calluna vulgaris*, tend to produce large numbers of seeds and not necessarily because seed survival is better in acid soils. Other studies have reported a trend for lower seed numbers in more acid soils. For example, Hill & Stevens (1981) found that the number of viable seeds present was higher in mineral soils than in peat; although they suggested that this may have been because the impermeability of the peat causes seeds to remain near the surface, where conditions are less favourable for survival. Staaf et al. (1987) also found fewer seeds and species in the seed banks of more acid beech forest soils in Sweden. However, this was mainly because many of the species in the seed banks and ground flora at the more fertile, basic sites did not occur at the more acid sites. A number of studies on agricultural soils (eg. Lewis, 1961; Schafer & Chilcote, 1970) indicate that seed survival is improved by cold anaerobic conditions, such as those occurring in wet soils. Chippindale & Milton (1934) also observed higher numbers of viable seeds in water-logged soils in their study of pasture seed banks. Since germination accounts for much of the loss of seeds from the soil, greater rates of loss would be expected under conditions favourable to germination, ie. near the soil surface in moist, warm, well-aerated soil.

1.5.3. Heterogeneity within the Seed Bank

Relatively few studies have set out to ascertain the spatial pattern of seeds in the soil. Most of these have employed either random soil cores (eg. Schenkeveld & Verkaar, 1984) or transects of contiguous cores (eg. Kellman, 1978). However, the number of cores employed generally has been too small to determine the small-scale pattern of distribution of seeds in the soil.

Thompson (1986) investigated spatial pattern in a pasture seed bank by the complete evaluation of the number and distribution of seeds in a small area of soil. This study revealed significant clustering of the main species in the seed bank (*Agrostis capillaris* and *Danthonia decumbens*). Bigwood & Inouye (1988) developed a mathematical method of spatial pattern analysis to investigate the seed bank of an old field and found that all the species had clustered distributions, but the patterns of clustering were irregular.

The seed input at any particular point may be influenced, for example by the distance from seed sources, seed production, seed dispersal mechanisms and the activities of dispersal agents. Although long-distance seed dispersal occurs, local seed dispersal predominates. Sometimes, seeds are dispersed as a group for example, the seeds of *Juncus spp.*, which are mucilaginous and tend to stick together (Richards & Clapham, 1941). In germination trials, Granstrom (1982) observed clusters of up to 20 seedlings of *Vaccinium myrtillus*, which were obviously derived from single berries. The post-dispersal movement of seeds may cause seeds to become aggregated, for example as a result of accumulation in depressions or cracks. Many seeds, particularly those of woodland species, are dispersed by ants (Kjellsson, 1985, 1988), resulting in high concentrations of seeds near ant nests. The implications of seed bank heterogeneity for sampling are considered in section 3.2.1.

1.5.4. Seed Bank Types

Thompson & Grime (1979) recognized two categories of seed banks; transient (Types I and II), in which no seeds remain viable for more than one year, and persistent (Types III and IV), in which some seeds remain viable for longer than one year.

Type I species are mostly large-seeded grasses which germinate in the autumn following shedding, for example *Arrhenatherum elatius* and *Lolium perenne*. The seeds of these species are therefore absent during the winter and early spring. Those of Type II species require a period of chilling before germination can take place (Grime et al., 1988). After chilling, the seeds germinate, in light and in darkness, over a wide range of temperatures and rapid germination may occur, even at low temperatures (Thompson & Grime, 1979). Type II species are typically large-seeded forbs such as *Hyacinthoides non-scripta*, *Mercurialis perennis*, *Oxalis acetosella* and *Galium aparine*. Both Type I and Type II species have transient seed banks.

In contrast, Type III and Type IV species have persistent seed banks, the seeds of these species are present in the soil throughout the year. Examples include *Poa annua* (a Type III species) and *Juncus effusus* (a Type IV species). Type III and Type IV species differ in the proportion of the annual seed input which enters the buried seed bank. This is small for Type III species and large for Type IV species.

Species with persistent seed banks are generally light-demanding and characteristic of open habitats, germination is often inhibited by darkness (Grime & Jarvis, 1975; Grime et al., 1981) and the seeds tend to be small and therefore easily buried (Thompson, 1987).

The seeds of short-lived (Types I and II) species may germinate at depths unsuitable for emergence. The buried seeds of long-lived (Types III and IV) species are less likely to germinate in unsuitable conditions, for example van Baalen (1982) recorded no losses for seeds of *Digitalis purpurea* buried in cloth bags over a period of two years.

Since the seeds of species with Type III and Type IV seed banks often remain viable in the soil for periods considerably longer than one year, Bakker (1989) has suggested a further category of permanent seed banks. This refers to species whose seeds survive for longer than five years in the soil. Grasses often have transient seed banks although some have permanent seed banks, for example *Agrostis spp*. The seed banks of *Poa spp*. and *Holcus lanatus*, classified as persistent by Thompson & Grime (1979) are relatively short-lived and probably not permanent. Species with permanent seed banks include *Juncus spp*., *Carex spp*., *Digitalis purpurea* and *Calluna vulgaris*.

Nakagoshi (1985) recognized three categories of seed bank (A, B and C), which are similar to Types II, III and IV, of Thompson & Grime (1979). He also differentiated species into nine functional groups on the basis of their seed bank characteristics. The species described in this study are those of temperate forests in Japan, although European and North American species can be similarly classified.

1.5.5. The Importance of Seed Banks to Conservation

Moore (1983) has raised the question of how the extinction of a plant species from a site is defined, given the existence of seed banks. For example, Rowell et al. (1982) described the germination of *Viola persicifolia* from soil samples collected at Wicken Fen in Cambridgeshire, where this species had supposedly been extinct for over 60 years. Rowell (1984) subsequently observed natural populations of this species which had presumably originated from buried seed following disturbance.

Seed banks can be the major source of regeneration of undesirable species, for example the majority of species in the seed bank in arable soils are those of annual weeds (Roberts, 1981). However, buried seeds can also have important implications for conservation management where required or preferred species have been lost from the vegetation but survive in the seed bank.

Freshwater wetlands can be managed by lowering their water levels (drawdowns) to recruit species from the seed bank (van der Valk, 1981). The use of drawdowns as a management practice was developed mainly to restore species which had been eliminated by high water levels or overgrazing (van der Valk & Pederson, 1989).

Species with long-lived seeds predominate because they survive years of high water as seeds and become re-established in the vegetation during the next drawdown, or because they survive the drawdown as seeds and become re-established when standing water returns (van der Valk, 1981).

The presence of long-lived seeds of heathland species in soils can be used to restore improved or degraded heathland. In northern Belgium, Stieperaere & Timmerman (1983) found seeds of *Calluna vulgaris*, *Erica tetralix*, *Potentilla erecta* and *Luzula multiflora* beneath improved grassland reclaimed from heath 20 years previously. In the Netherlands, heath invaded by grasses can be restored by sod-cutting, which removes the grass seed bank, exposing the more deeply buried seeds of the heathland species (Diemont, 1990). If the seed bank no longer exists, recolonisation is slow. This has been illustrated by Salonen (1987) who found that where peat-cutting in Finland had removed the seed bank, vegetation recovery was slow and reliant on wind-dispersed species, such as *Eriophorum vaginatum* and *Pinus sylvestris*.

Seed banks are less useful for the restoration of plant communities in which the species of value have short-lived seeds. For example the species-poor tall grassland which develops from chalk grassland lacks species such as *Thymus praecox*, *Gentianella amarella* and *Prunella vulgaris* and these species are also absent from the seed bank (Jefferson & Usher, 1987).

In neglected coppice woodlands the seeds of shade-tolerant species such as *Hyacinthoides non-scripta* and *Anemone nemorosa* are absent from the seed banks. It is therefore important that, whatever form of management is applied to old coppicewoods, these species are not lost from the ground flora (Brown & Oosterhuis, 1981).

1.6. WOODLAND SEED BANKS

A number of studies have been carried out to investigate woodland seed banks, the results of which are summarised below.

1.6.1. Coppice Seed Banks

Salisbury (1924) described the appearance of ground flora species associated with the open phase of the coppice cycle (plants typical of woodland edges which he called "marginal" species) as a process of "ebb and flow". He assumed that species excluded by the shade of a dense canopy survived in open areas such as clearings and rides from where they would recolonise a cleared area after coppicing. Rackham (1975) described two species (*Juncus spp.* and *Centaurium erythraea*) which he thought could survive in the soil of the coppice area as dormant seed, reappearing in the vegetation after each clearance. Brown & Oosterhuis (1981) established that many other species can survive as buried seed during the dark phase of the coppice rotation. Germination from the seed bank appears to be the main method by which species establish themselves after cutting. Thus, Salisbury's concept of recurrent invasion does not apply if cutting is regular. In neglected coppice, however, species are lost from the seed bank and the importance of openings in the canopy for species survival will increase. On clearance of the canopy, these areas may act as seed sources in the way described by Salisbury (1924).

Brown & Oosterhuis (1981) sampled soils from densely shaded areas of neglected coppice in south east England, where coppicing had not taken place for 30-40 years. The ground flora was absent or sparse, consisting of shade-tolerant species such as *Mercurialis perennis*, *Oxalis acetosella* and vernal species such as *Hyacinthoides non-scripta*, *Ranunculus ficaria*, and *Anemone nemorosa*. None of these species was present in the seed bank. In contrast, the most abundant species in the seed bank, *Betula spp*., and *Juncus effusus*, were absent from the ground flora. Only *Rubus fruticosus* was present in both the ground flora and the seed bank.

Harris (1986) investigated the seed banks of neglected coppice and Bradford Plan units on the Tavistock Woodlands Estate as part of a study examining the ecological benefits of the Bradford Plan forestry management system. Most of the coppice species had been lost from both the ground flora and seed bank of oak coppice after 70-80 years of neglect but still remained in a dense-canopied coniferous plantation with Bradford Plan units. The implication is that, provided the period of neglect or coniferisation has not been too long, ie. less than 50 years, the opening of the canopy which occurs when Bradford Plan units are introduced helps to maintain the diversity of the ground flora and seed bank (Harris & Kent, 1987b).

Another study based in the Tavistock Woodlands Estate (Darby, 1987) found that in old coppice, species with relatively short-lived seeds, such as *Veronica officinalis*, *Plantago major* and *Ulex europaeus*, were absent from the seed bank after 70 years of neglect. After 100 years, only two species, *Digitalis purpurea* and *Hypericum pulchrum* remained and after 200 years, only *Hypericum*.

1.6.2. Plantation Seed Banks

The presence of a seed bank of mainly light-demanding species in the soils of plantations has been demonstrated in a number of studies. For example Granstrom (1988) found very high seed densities of *Calluna vulgaris* in the soils of afforested heathland sites in Sweden. Seeds of *Carex pilulifera* and *Juncus spp.* were also abundant. None of these species was present in the ground flora of the plantations studied. Hill & Stevens (1981) also reported high densities of *Calluna vulgaris* seeds in the soils of conifer plantations in the British uplands. Seeds of *Carex spp.*, *Galium saxatile* and *Juncus spp.* were also abundant. The ground flora was sparse or absent in the stands examined. In both studies, the species which were abundant in the seed banks were absent from the ground flora and had originated from the heathland vegetation present at the sites before afforestation. Another species which has been shown to survive as buried seed for long periods of time in plantation soils is *Luzula pilosa* (Granstrom, 1982). *Luzula pilosa* only produces seed prolifically during the first few years after clear-felling, yet appreciable buried seed densities of this species were found in a mature (120 year-old) conifer stand in Sweden.

1.6.3. Absence of Tree Seeds from Woodland Seed Banks

Seeds of the dominant tree species are generally poorly represented in the seed banks of plantations and temperate woodlands (Hayashi & Numata, 1964; Frank & Safford, 1970; Kellman, 1970, 1974; Strickler & Edgerton, 1976; Whipple, 1978; Hill & Stevens, 1981; Thompson & Grime, 1979; Pratt et al., 1984; Staaf et al., 1987). Most tree seeds are relatively short-lived and often subject to high rates of predation.

1.6.4. Species Composition of Woodland Seed Banks and Ground Flora

A general lack of correspondence between the species present in the ground flora and those in the seed banks has been reported in a number of studies of plantations and temperate woodlands (Karpov, 1960; Petrov, 1977; Thompson & Grime, 1979; Brown & Oosterhuis, 1981; Hill & Stevens, 1981; Petrov & Palkina, 1983; Staaf et al., 1987; Granstrom, 1988). This is mainly because the light-demanding, early successional species, with long-lived seeds, have been lost from the ground flora. Shade-tolerant species are frequent in the ground flora but the transient seeds of these species are absent from the seed banks, or if present, are difficult to detect. These species may also produce little seed in dense shade.

In old undisturbed woodlands, the seed banks become depleted (Piroznikow, 1983; Petrov, 1987) since the seeds of the light-demanding species, although long-lived, are not immortal. The seed banks of these woodlands are small and composed of species with transient seeds, which are also present in the ground flora, and species with wind-dispersed seeds.

Brown & Oosterhuis (1981) concluded that germination from the seed bank was the main method by which species establish themselves after coppicing. Experimental studies such as that of Marks & Mohler (1985) have demonstrated the importance of the seed bank in the early stages of old field succession. In their study, the vegetation was removed either by cultivation (control plots), treatment with herbicides (buried seed plots) or steam sterilization (sterilized plots). The latter treatment also killed all the buried seeds and vegetative fragments. Vegetative fragments were removed from the buried seed plots and vegetative colonisation of both the buried seed and sterilized plots from the edges was prevented. The control plots were colonised vegetatively from the edges and from buried seeds and vegetative fragments. By the middle of the second growing season the vegetation of these plots was similar to the surrounding field. In the buried seed plots, species germinating from the seed bank had established a moderately dense cover by the end of the second season. Virtually nothing had grown on the sterilized plots by the end of the second season.

No similar studies have been carried out in temperate woodlands but in tropical forests, Uhl et al. (1981) and Lawton & Putz (1988) investigated the role of the seed bank in vegetation recovery following slash and burn, by killing seeds in the soil with methyl bromide. Both studies showed that most of the woody colonising species originate from the seed bank. A study by Young et al. (1987) also demonstrated the overwhelming importance of the seed bank in the colonisation of a cleared forest site in Costa Rica.

1.7. WOODLAND GROUND FLORA

A further aim of this thesis is to examine the ground flora under a range of forest and woodland types. The diverse ground flora associated with ancient woodlands is one feature which makes them important sites for nature conservation; particularly since many of the species characteristic of ancient woodland do not readily colonise new plantations. Carpets of woodland flowers such as bluebells (*Hyacinthoides non-scripta*) have always been appreciated, for example in describing a planted wood, Sir Hugh Beevor (Beevor, 1925; quoted by Peterken, 1981), remarked... "but how much does it fail to charm compared with an ancient wood with all its glory of bluebells".

The ground flora of a wood depends on its location, the climate and soil type as well as past and present management. In any one stand, the flora will change over time as different stages of the rotation are reached and the level of stocking changes. The effects of forestry practices on woodland ground flora have been discussed in a detailed literature review by Mitchell & Kirby (1989) and Mitchell (1991). The following section provides a brief summary these effects.

1.7.1. Ground Flora of Coppice and Coppice-with-Standards

Hayley Wood in Cambridgeshire is a nature reserve in which a series of coppice plots have been cleared to demonstrate the effect of traditional coppice management (Rackham, 1975). The ground flora of coppicewoods in south east England has been described by Ash & Barkham (1976) and Ford & Newbould (1977). In contrast to the flora of plantations, a diverse flora can survive in coppicewoods. Coppicewoods tend to have areas at all stages of the rotation, producing a diversity of habitats. Diversity within the wood is increased further if the areas (coupes) cut each year are small. The short rotation, 5-30 years, as compared with 50-150 years for high forest, means that open phases occur more frequently and the ground flora has to survive fewer years under a closed canopy than in a plantation.

During the shade phase, towards the end of the coppice rotation, the field layer is generally poorly developed, consisting of shade-tolerant species. In the first season after coppicing, surviving species begin to grow more vigorously. In the second season after coppicing, the shade flora grow and flower with even greater vigour and other species become established. At this stage, the coppice shoots are 1-2 m tall and in each subsequent season, their height and productivity increase. As the coppice regrows, there is a corresponding decline in vigour of the ground flora.

There are a number of ways in which the ground flora can survive the shade phase (Rackham, 1975; Peterken, 1981). Some species are shade-tolerant, for example *Ajuga reptans* and *Galeobdolon luteum*. Vernal species flower in the spring, before the canopy is in leaf, for example *Anemone nemorosa*, *Hyacinthoides non-scripta*, *Primula elatior* and *Ranunculus ficaria*. Shade-intolerant species, for example *Digitalis purpurea* and *Juncus effusus*, survive as buried seed, germinating in response to the disturbance caused by coppicing. Marginal species survive along rides and in clearings and only occur in recently cut coppice. Casual species, such as *Anagallis arvensis* and *Chamaenerion angustifolium*, colonise from outside the wood. Some species may survive in several of these ways, for example *Rubus fruticosus* is a shade-tolerant species which also has a seed bank. Another example is *Cirsium palustre*, which is abundant in the first years after coppicing and may be classified as a marginal species. However, the persistence of the species in Dutch ash coppice woodlands has been shown by Pons & During (1987) to be partly dependent on its ability to form a long-lived seed bank. The vernal species provide spectacular displays of colour, particularly in the second season after coppicing. Coppicing favours these species since competing species which grow in the summer are suppressed during the shade phase.

1.7.2. Ground Flora of Neglected Coppice

In neglected coppice, marginal and casual species are reduced or eliminated from the ground flora, particularly if rides become overgrown. The seed bank species can survive as buried seed for long periods but in the absence of disturbance, no renewal of seed populations occurs and species are eventually lost. Summer-growing species amongst the shade flora may increase at the expense of the spring-flowering species which can no longer compete.

Deliberate conversion of coppice to high forest normally involves planting, usually with conifers. The changes which take place as a result are similar to those which follow afforestation.

1.7.3. Ground Flora of Plantations

During the establishment phase, the initial response of the ground flora is as if coppicing has taken place. However, once canopy closure occurs, the ground flora becomes impoverished and remains so until clear-felling. The spring-flowering species are lost except at the woodland margins. Some species are able to survive the length of the rotation in the ground flora or as buried seed. Marginal and casual species are less affected.

A number of studies have described the ground flora of plantations by comparing stands of different ages at different sites, for example Ovington (1955), Hill (1979a) and Kirby (1988). An alternative way of recording changes within plantations is to sample the same stands over time. Studies which have done this include those of Hill & Jones (1978) and Anderson (1979), who re-surveyed the plots first described by Ovington (1955). The ground flora of conifer plantations is usually limited, partly because plantations are often established on acid and infertile sites. After felling, the ground flora consists of species already present at the site and those germinating from buried seed or wind-dispersed seed (Hill & Stevens, 1981). The early stages are similar to coppice but the species-rich ground flora becomes increasingly depleted as the canopy closes. At 10-15 years, the dark "thicket" stage is reached, intense shade and the smothering effect of the litter reduce the ground flora to a minimum. As the forest matures and thinning is carried out, some of the ground flora species may begin to reappear. However, in Britain this stage is shortened as little conifer forest is allowed to grow to full maturity. The normal rotation length in state forests is 55 years. In western and upland regions, felling is often carried out earlier (as early as 30-35 years) as windthrow risk increases with the age and size of the tree.

1.7.4. Aspects of Silvicultural Systems which affect the Ground Flora

Stocking density

Differences in stocking densities affect the ground flora. Nihlgard (1970) compared the ground vegetation in stands of Norway spruce in Sweden with different stocking densities. The dominant species was *Oxalis acetosella* in the densest stand but *Deschampsia flexuosa* in the least dense. Sakura, Gimingham & Millar (1985) also recorded an increase in the abundance of *Deschampsia flexuosa* in thinned larch stands in Scotland and the appearance of other grasses (*Anthoxanthum odoratum*, *Festuca ovina* and *Holcus mollis*) in the least densely stocked stands. Light is probably the main factor causing differences in ground flora between stands of different stocking densities. In addition, high tree density is associated with high root competition and an increase in the thickness of the litter layer due to higher rates of litter fall and reduced rates of decomposition. The ground flora is suppressed by both lack of moisture and the smothering effect of the litter.

Tree species

Tree species and ground flora are usually associated because they have site requirements in common. Several studies of the plots used by Ovington (Ovington, 1955; Anderson, 1979; Page, 1981, 1983) have indicated that no ground flora species can be closely associated with any one tree species or even with conifers or broadleaves. The elimination of species at the thicket stage affects the composition of the ground flora in the later stages of the rotation. Broadleaves, with the possible exceptions of beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*), tend not to completely eliminate the ground flora. Spruces (*Picea spp.*) and firs (*Abies spp.*) normally have bare ground at the thicket stage but under pines (*Pinus spp.*) and larches (*Larix spp.*) some ground flora usually survives (Hill & Jones, 1978; Hill, 1979a). After the thicket stage, the ground flora may increase, often considerably under pines, larches, Douglas fir (*Pseudotsuga menziesii*), most broadleaves and even, in terms of number of species, under Norway spruce (*Picea abies*) and Grand fir (*Abies grandis*) (Anderson, 1979). In a well-thinned spruce wood, there is likely to be a patchy cover of shade-tolerant grasses and ferns, such as *Deschampsia flexuosa* and *Dryopteris dilatata*. In well-thinned pine and larch woods, there is often a dense growth of grasses and ferns, especially *Pteridium aquilinum* and *Dryopteris dilatata*, with much *Rubus fruticosus* in lowland plantations on more fertile soils (Hill, 1979a, 1986).

Management practices

Felling and site preparation may cause extensive disturbance but the ground flora is not usually completely eliminated. McComb & Noble (1982) compared the ground flora in a mixed broadleaved stand with that in an adjacent pre-thicket stage conifer plantation, where site preparation had been intensive. The broadleaved stand contained many species which were absent from the plantation. The plantation flora was dominated by early successional species, but included some species which had survived the disturbance. Drainage also affects the vegetation; wetland species such as *Pinguicula vulgaris* and *Menyanthes trifoliata* disappear as conditions become drier. Fertilizers generally benefit the more vigorous species, such as *Rubus fruticosus*, and high phosphate levels encourage the growth of *Urtica dioica*. A diverse ground flora is generally associated with a low level of soil nutrients. Weeding also affects the ground flora, particularly if herbicides are used.

Management practices can to some extent be modified in the interests of conservation, for example by the use of less intensive site preparation. However, with the clear-fell system it is not possible to avoid the inimical thicket stage, which is an essential phase in the growth of the stand. The onset of the thicket stage can be delayed by planting at a wider spacing and its duration shortened by early thinning but it cannot be avoided altogether.

1.8. CONCLUSION

The purpose of this introductory chapter has been to set out the aims and objectives of the thesis, provide appropriate background material and review the relevant literature. The starting point of the research was a pilot study at the Tavistock Woodlands Estate in Devon. This pilot study is described in chapter two.

CHAPTER TWO : A PILOT STUDY OF THE BRADFORD PLAN FORESTRY MANAGEMENT SYSTEM

2.1. INTRODUCTION

In this chapter the pilot study is described. This was carried out in the first year of the project, at the Tavistock Woodlands Estate. The implications of the results of the pilot study to the main study are discussed.

2.2. PILOT STUDY

2.2.1. Aims

The aim of the pilot study was to gain experience in the basic techniques of seed bank sampling and enumeration and to develop a suitable sampling programme for use in the main survey. The pilot study also provided an opportunity to make a preliminary investigation of seed bank heterogeneity and ground flora diversity associated with the Bradford Plan (B-Plan) forestry management system described in section 1.4.1. and to evaluate methods of data analysis.

2.2.2. Site Description

The pilot study was carried out at Carthamartha Wood (O. S. Grid Ref: 378 776, Sheet number 201). The wood was bought by the Duke of Bedford in 1870 and is part of the Tavistock Woodlands Estate, for which records of woodland management have been kept since the 16th century. The existing oak coppice was cleared in 1906 and replanted with a mixture of beech (*Fagus sylvatica*), Scots pine (*Pinus sylvestris*), Douglas fir (*Pseudotsuga menziesii*) and larch (*Larix spp.*). Conversion to the B-Plan forestry management system began in 1962. At the time of sampling (1987/1988), the oldest sub-units, planted with Western red cedar (*Thuja plicata*), were 26 years old and the next oldest, planted with Western hemlock (*Tsuga heterophylla*), 20 years old. The youngest sub-units (Western red cedar) were 8 years old, due to a gap in the six-yearly planting schedule. In 1984, in order to raise money for death duty payments, B-Plan planting was abandoned and all remaining trees from the previous rotation were felled. Douglas fir was planted between existing sub-units in 1985. Thus four canopy stages were present (Figure 2.1. and Plate 2.1.).

2.2.3. Methods

Field methods

The seed bank survey was carried out in November 1987 and the ground flora was surveyed in the following June. Five B-Plan units (plus adjacent 6 m x 6 m squares in the cleared and replanted areas) were sampled (Figure 2.2.). For the seed bank survey, four regularly spaced 20 cm x 20 cm (400 cm^2) samples were collected from each of the B-Plan sub-units and from the cleared areas, making a total of 80 litter and 80 soil samples. The soil samples (from the 0-5 cm layer) were collected using a spade and trowel. For the ground flora survey, two 1 m^2 quadrats were randomly located in each sub-unit and in the cleared areas, making a total of 40 quadrats. Percentage cover values for the ground flora species, litter, bare soil and rock were recorded.

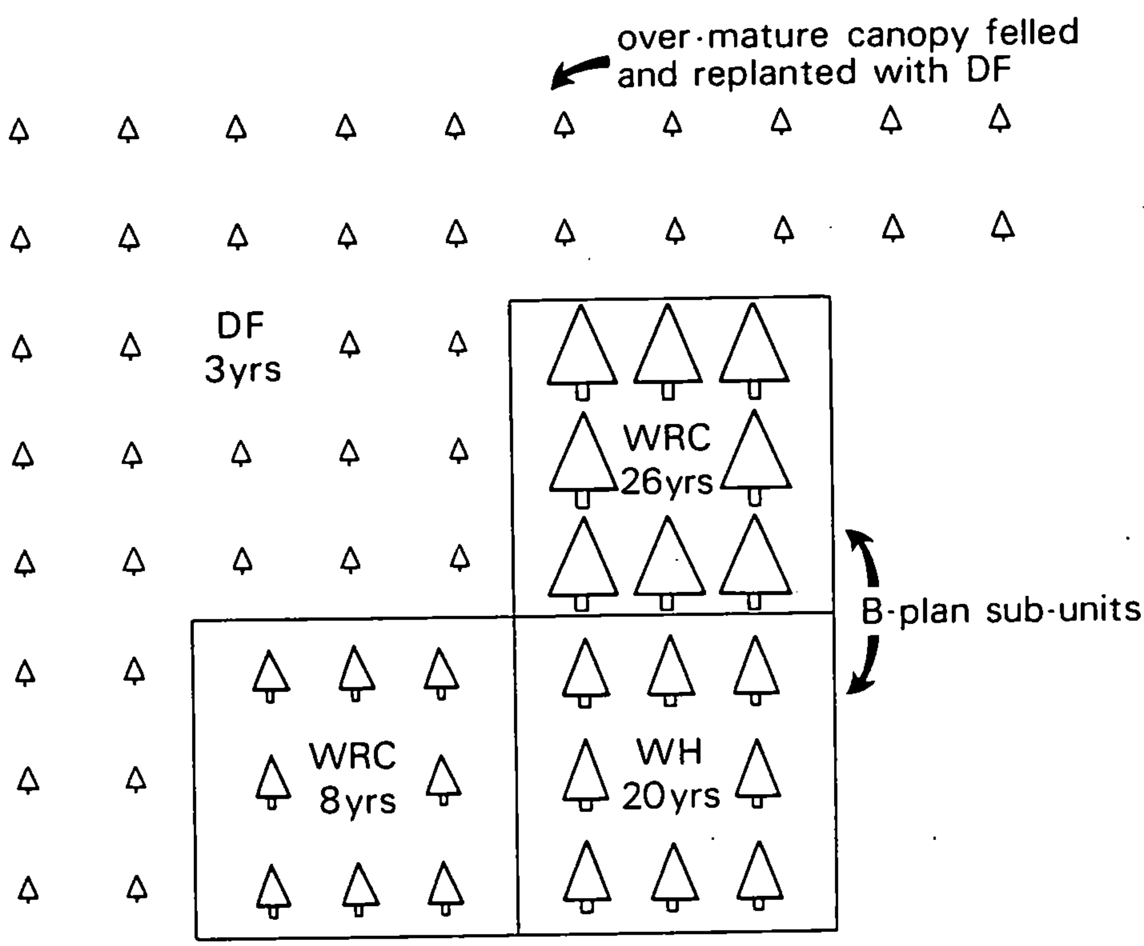
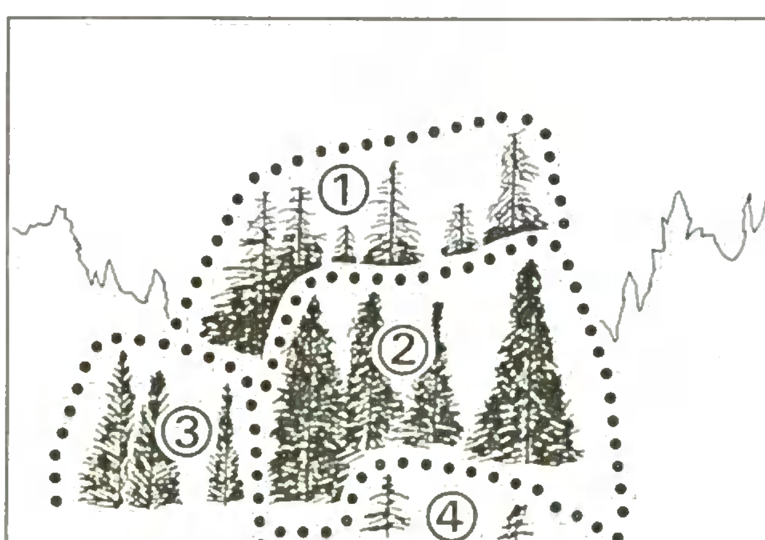


Figure 2.1. Schematic diagram to show Bradford Plan planting at Carthamartha Wood.

Plate 2.1. A Bradford Plan unit at Carthamartha Wood. The four canopy stages can be distinguished.



① WRC 26 yrs
② WH 20 yrs
③ WRC 8 yrs
④ DF 3 yrs

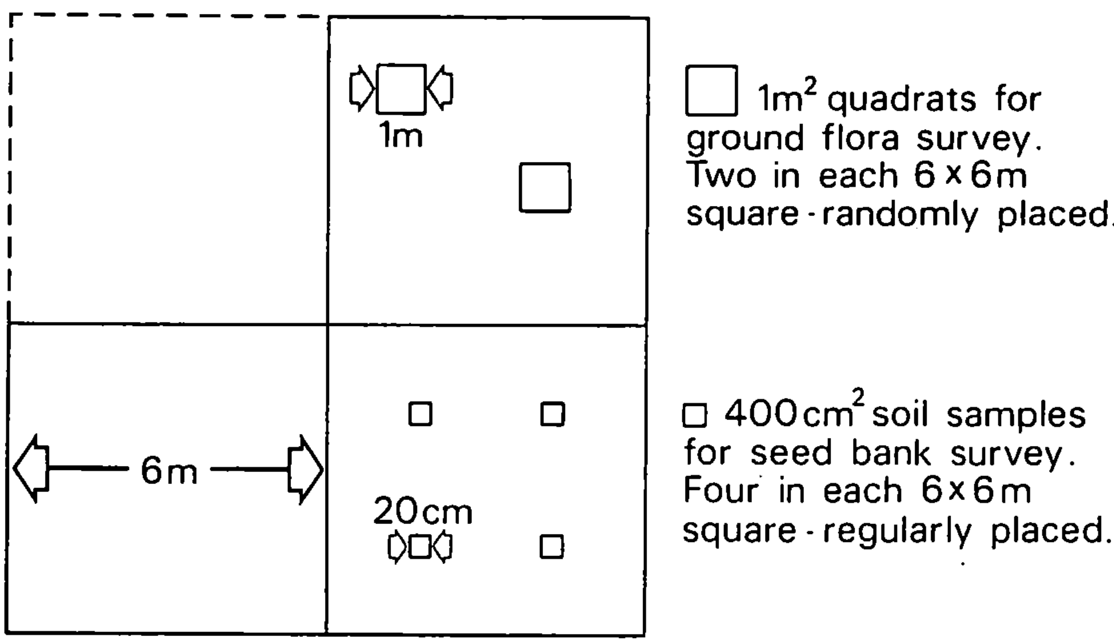


Figure 2.2. Pilot Study: Location of quadrats and sampling points in a Bradford Plan unit at Carthamartha Wood.

Germination trials

The samples were too bulky to fit into standard size seed trays, so half of each sample was discarded, making the sample size effectively 20 cm x 10 cm (200 cm^2). Stones and roots were removed from the soil with the use of a coarse (1 cm) sieve. The samples were spread out in the seed trays on a layer of sand, placed in an unheated greenhouse and watered regularly (Plate 2.2.). Several control trays containing only sand were used to trap any wind-dispersed seed.

The optimum time to collect soil samples is in the spring, when seeds have undergone natural stratification during the winter. Since the samples were collected in the autumn, before natural chilling occurred, the effect of artificial chilling on seed germination was investigated. To do this, the unused half samples from one B-Plan unit were chilled at 5°C for eight weeks before being transferred to the greenhouse. Once germination began, seedlings were identified and removed at intervals over a two month period. Any seedlings which could not be identified were transferred to individual pots and grown on until identification was possible (Plate 2.3.). Although, to ensure a complete enumeration, it is necessary to extend the period of recording over one or two years, for the purposes of this preliminary study, a shorter recording period was sufficient to provide the required information on seed bank heterogeneity.

Estimation of seed densities

The total surface area sampled for each of the four B-Plan stages was 4000 cm^2, so seed densities (seeds.m^{-2}) were estimated by multiplying the number of seeds germinating from the samples by 2.5.

Plate 2.2. Pilot Study: Soil samples in the greenhouse. Trays containing sand and compost were used as controls.


Plate 2.3. Pilot Study: Seedlings grown on for identification.

2.2.4. Results

Ground flora survey

Table 2.1. shows the species present in the ground flora in the four different canopy stages. The ground flora in the two oldest sub-units was sparse and only shade-tolerant species were present. A noticeably more diverse ground flora was present in the more open youngest sub-units and in the cleared areas. Some remnants of the earlier ground flora survive in the older sub-units, for example small individuals of *Viola riviniana* and *Hypericum pulchrum*, due to increased light levels in the sub-units compared with those in clear-fell plantations of the same age.

In order to examine the quadrat and species groupings, the data were analysed using TWINSPAN (TWo-way INdicator SPecies ANalysis), Hill (1979b) and DECORANA (DEtrended CORrespondence ANAlysis), Hill (1979c). Standard cut levels (0, 2, 5, 10 and 20) were used, as these are suitable for percentage cover data of British woodland flora. The TWINSPAN classification is shown in Table 2.2. Seven groups of quadrats can be distinguished, representing a gradient in species abundance and composition from the sparse, species poor ground flora of the oldest sub-units to the more abundant and diverse ground flora of the cleared areas. The first group (group A) is distinct from the others as it is the only group in which *Blechnum spicant* is present and only two species (*Hedera helix* and *Rubus fruticosus*) occur frequently. The second group (group B) is characterised by the additional presence of *Lonicera periclymenum* and the third (group C) by both *Lonicera periclymenum* and *Pteridium aquilinum*. Group D is distinguished from group C by a reduction in the presence of *Hedera helix* and the appearance of *Hyacinthoides non-scripta*. Groups E, F and G

Table 2.1. Pilot Study: Species in the ground flora in the four canopy stages at Carthamartha Wood. Tree and shrub species have been included only where seedlings were present.

Species	WRC 26 yrs	WH 20 yrs	WRC 8 yrs	DF 3 yrs
Agrostis spp.	-	-	+	+
Betula spp.	-	-	+	+
Blechnum spicant	+	-	-	-
Calluna vulgaris	-	+	-	+
Carex pilulifera	+	+	-	+
Carex pendula	-	-	-	+
Digitalis purpurea	-	-	-	+
Dryopteris dilatata	-	-	+	-
Galium saxatile	-	-	-	+
Hedera helix	+	+	+	+
Holcus lanatus	-	-	-	+
Hyacinthoides non-scripta	-	-	+	+
Hypericum pulchrum	+	+	-	+
Ilex aquifolium	-	-	-	+
Juncus bufonius	-	-	+	+
Juncus effusus	-	-	+	+
Lonicera periclymenum	+	+	+	+
Luzula multiflora	-	-	-	+
Luzula pilosa	+	+	+	+
Oxalis acetosella	-	-	+	-
Pteridium aquilinum	-	+	+	+
Rubus fruticosus	+	+	+	+
Viola riviniana	+	-	+	-
Total no. of species	8	8	13	19

```
                               quadrats
                1 3  223 122 113121113  3322311223334  2
                0941256346783196802375567829045141290783

 1 BLEC SPIC    33--------------------------------------  000
23 QUER SPP     --------3---2---------------------------  000
27 TSUG HETE    --------2----2--------------------------  000
28 BARE SOIL    ---3---3-2--2---223-3---3---------------  000
 9 HEDE HELI    322232332222-222-122222-------22-22-----  001
15 LUZU PILO    31-----2-3-2-2--3-22--------2--2-----2  001
31 LOGS         24-3434-445543--32-----4--4------2---4-4  001
29 LEAF LITT    5555555554555555555555555555555555555--5  010
30 MOSS         2334334455555534534454554345555554554555  010
 2 DRYO DILA    -----------------------3-4--4-----------  0110
14 LONI PERI    --------232423212233--554444444334--2-3  0110
17 RUBU FRUT    --2-2323242332213224325443445344 4-344543  0110
18 VIOL RIVI    2-----------------------------2---------  0111
26 THUJ PLIC    -43----3--------3-2-------44--2---------  0111
 3 PTER AQUI    -------------34-324533--555-455545555--4  10
 4 CALL VULG    ---------3-------1---1----------4-----3  10
22 FAGU SYLV    2---------3------2-42-----3-3--24-------  10
19 AGRO CAPI    ---------4---------2----------------433-34  1100
25 PSEU MENZ    ---------3--------------------------2-4---4-  1100
 6 CARE PILU    --------------2-2-------------33-----2--  1101
10 HYAC NONS    ----------------------33--222--2332--322  1101
11 HYPE PULC    --2-------3-----1-1--------2-232343-2232  1101
32 STUM         ------------5344----------4-5443-43-3-  1101
21 BETU SPP     --------------------------3-2-4-32---23-  11100
 5 CARE PEND    ----------------------------------33445---  11101
12 JUNC EFFU    ----------------------------322342434--3  11101
13 JUNC BUFO    -------------------------------3---55---  11101
16 OXAL ACET    -------------------------------3--------  11101
 7 DIGI PURP    -------------------------------------2--  1111
 8 GALI SAXA    --------------------------------2----33  1111
20 HOLC LANA    --------------------------------3----555  1111
24 ILEX AQUI    --------------------------------------4-  1111

                0000000000000000000000000011111111111111
                0000000000001111111111111100000000000111
                0000000011110000000000111100000000111
                01111111    0000111111    00000011
                 0011111        001111    000111
                   00001

groups             A    B      C       D     E     F  G
```

Key

% cover	abundance
0	-
1 - 2	1
3 - 5	2
6 - 10	3
11 - 20	4
> 20	5

Table 2.2. Pilot Study: TWINSPAN classification of ground flora data from Bradford Plan units at Carthamartha Wood.

are characterised by the presence of *Hyacinthoides non-scripta, Hypericum pulchrum* and *Juncus effusus*. Groups F and G are distinguished from group E by the more frequent occurrence of grasses (*Agrostis capillaris* and *Holcus lanatus*) and group G from group F by the presence of *Digitalis purpurea, Calluna vulgaris* and *Galium saxatile*. In the DECORANA ordination plot of axis one against axis two, (Figure 2.3a.), the seven TWINSPAN groups have been amalgamated into four groups; group A, groups B, C & D, group E and groups F & G. These four groups correspond well with the groups obtained if the quadrats from the four canopy stages (Figure 2.3b.) from the different units are combined, indicating that the different ground flora types correspond with the canopy stages. No clear groups are seen when the quadrats from all canopy stages in the individual units are combined (Figure 2.3c.), indicating that the ground flora is not markedly different in any of the (replicate) units.

<u>Seed bank survey</u>

Tables 2.3. and 2.4. show the numbers of seedlings of different species which germinated in the tests. The same species were found in both the litter and the soil samples but the soil samples contained more seeds.

The seed data were also analysed using TWINSPAN and DECORANA, to determine whether distinct groupings (of seed numbers and species composition) could be identified within the seed bank and whether these corresponded with the ground flora groups found in the four canopy stages. The cut levels were reset to 0, 2, 5, 20 and 50. This was necessary to allow for the greater variations in seed abundances of the different species. The TWINSPAN classifications are shown in Tables 2.5. (soil samples) and 2.6. (litter samples). The classifications did not reveal any obvious

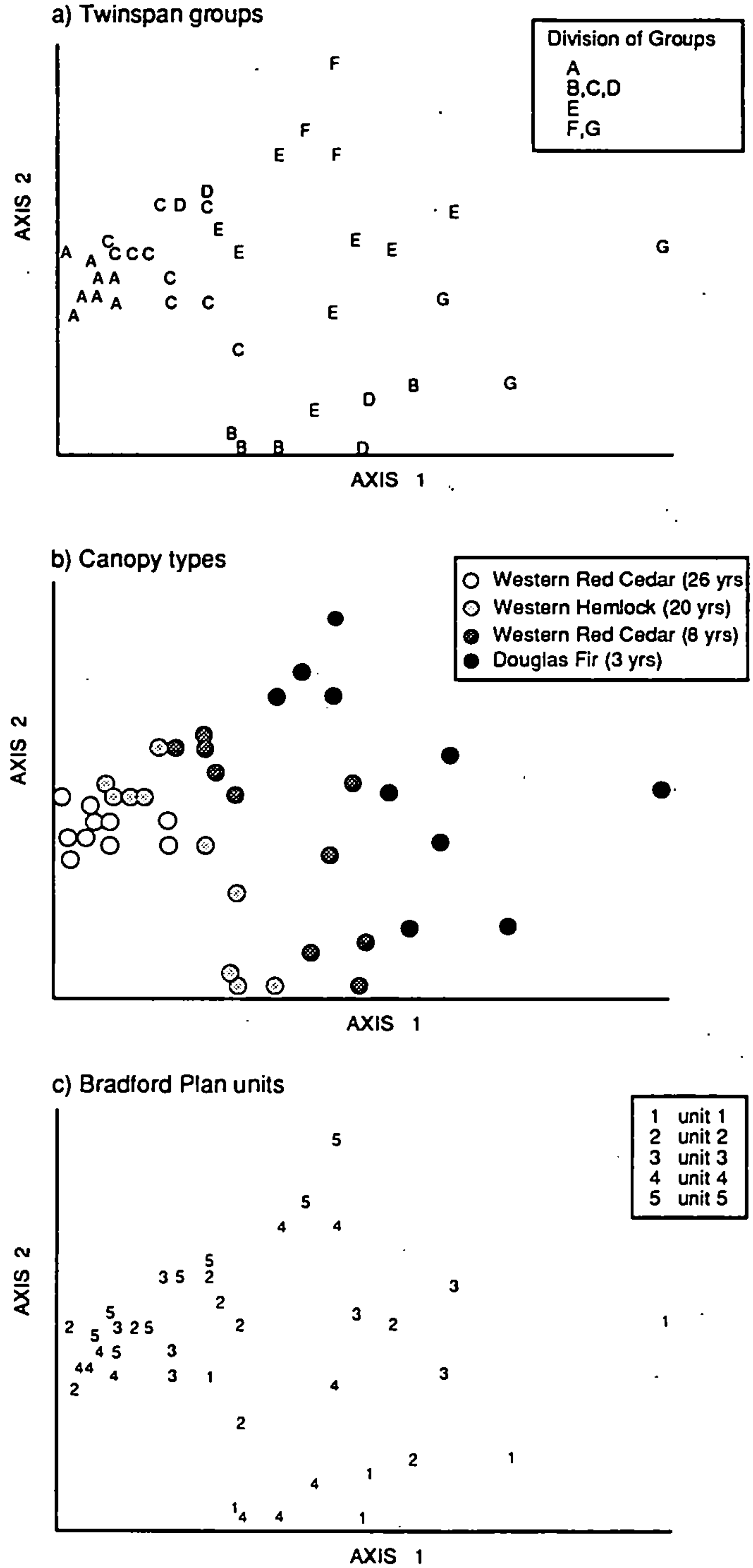


Figure 2.3. DECORANA ordination plots - ground flora survey
Pilot Study : Bradford Plan units at Carthamartha Wood

Table 2.3. Pilot Study: Number of seedlings in germination tests (soil samples).

Species	WRC 26 yrs	WH 20 yrs	WRC 8 yrs	DF 3 yrs
Agrostis spp.	19	21	173	265
Carex spp.	6	30	319	122
Digitalis purpurea	632	374	330	513
Hypericum pulchrum	600	370	296	369
Juncus effusus/bufonius	482	39	1063	308
Luzula spp.	165	105	346	109
Rubus fruticosus	112	307	374	321
Calluna vulgaris	6	1	-	2
Cymbalaria muralis	-	-	-	2
Epilobium spp.	8	3	16	32
Holcus lanatus	1	3	26	18
Hyacinthoides non-scripta	-	-	12	1
Lysimachia nemorum	-	5	27	-
Teucrium scorodonia	-	-	2	-
Veronica montana	2	1	16	-
Viola riviniana	1	1	6	-
Total no. of seeds	2034	1260	3006	2062
Seeds.m^{-2}	5085	3150	7515	5155
Total no. of species	12	13	14	12

Table 2.4. Pilot Study: Number of seedlings in germination tests (litter samples).

Species	WRC 26 yrs	WH 20 yrs	WRC 8 yrs	DF 3 yrs
Agrostis spp.	66	55	46	416
Carex spp.	2	14	38	246
Digitalis purpurea	54	31	18	203
Hypericum pulchrum	43	51	51	47
Juncus effusus/bufonius	258	23	75	152
Luzula spp.	137	47	165	250
Rubus fruticosus	44	78	29	27
Calluna vulgaris	1	3	-	-
Cymbalaria muralis	2	2	-	-
Epilobium spp.	15	38	9	150
Holcus lanatus	3	6	44	115
Hyacinthoides non-scripta	-	-	31	5
Lysimachia nemorum	-	-	1	-
Teucrium scorodonia	-	-	2	-
Veronica montana	-	-	1	-
Viola riviniana	-	-	1	-
Total no. of seeds	625	348	511	1611
Seeds.m^{-2}	1563	870	1278	4028
Total no. of species	11	11	14	10

```
                                                   quadrats
                 2222266334161222333344445573455663344445557 6 377727 277 617158  6  556711111 116
                 58627134678770493578356846099250812012401348970230354117269969015436785801239452

11 VIOL RIVI     -12-----1------------------------11------------------------------------------   000
14 LYSI NEMO     4-------------------------------------------------3------------------------------   000
15 TEUC SCOR     --2------------------------------------------------------------------------------   000
16 CYMB MURA     -------------------1-----------1---------------------------------------------------   000
 7 DIGI PURP     5443543555332534345535344532212222-3-11--212------32211234543352-2---1351-21--11   001
 8 LUZU PILO     5444414454-4-----32-3233-222213-321-32--11112-----2-344233--111---2---3-22443322   001
13 VERO SPP      3----------1-1-1---1-------------------------------------------------------3-----   001
 1 RUBU FRUT     -33331232413322213343344343322322334333233344133444233352-33321132333434443455342   01
 2 HYPE PULC     43333-3443554334445445333441 2-32233233331334412323255355245-34222334343333 4-331   01
12 CALL VULG     -----------3---------------------------1-------------11----------------1-----   01
 9 CARE PILU     2-321-2--------1--2-1-1-221-1-2------------21-221-2223232---134-------153552-333   10
 3 JUNC EFFU     --1-----------------------------------2-1----------1133-355355545423244345543-3-   110
 4 HOLC LANA     -2--------------------------------1--------------23-------11--1-----2--2--332---   110
 5 AGRO SPP      4432522--2--1--12-----3-111-11--------------311--1-121---1-234-3223222123-4342545   110
 6 HYAC NONS     -3--------------------------------------------------------2------12---------1   110
10 EPIL SPP      ----------12-----------------2-------------1-----------------2---------1232332-322   111

                 00000000000000000000000000000000000000000000000000000000001111111111111111111111
                 00000000001111111111111111111111111111111111111111111111110000000000000111111111
                 01111111110000000000000000000000000000000000000000111111110000011111111000000111
                  000000111000000000000000001111111111111111111111110011111100111000000010000001
                  011111     0011111111111111100000000000000000111111 000011      0001111 01111
                   01111       000001111111111100000011111111110011111

        groups   A    B            C                      D                E       F      G      H    I
```

Key

% cover	abundance
0	-
1 - 2	1
3 - 5	2
6 - 20	3
21 - 50	4
> 50	5

Table 2.5. Pilot Study: TWINSPAN classification of seed bank data (soil samples) from Bradford Plan units at Carthamartha Wood.

quadrats

```
                 55114 58177116717 233256 3344624722555 3577755  366677 36  264413334141244122026
                 8902367035945271894293107674750002956480313402128689263344517259451186778966815 3

 1 RUBU FRUT     1--2122-1--22-1--222222331--22-211323212212211333132232-1333---1-1--11121---------   000
 2 HYPE PULC     -2---2211323--1-------11111-----122123212211--233221343133-14-------22-------3--    000
 3 JUNC EFFU     21331153---2-21--2-----------------1-----------55---11-4213333-----------------5    000
11 VIOL RIVI     -------------------------1-----------------------------------------------------    0010
12 CALL VULG     -----------------------------------2------------1--1--------------------------    0010
16 CYMB MURA     ---------------------1---------1-1-------------1------------------------------    0010
10 EPIL SPP      --1---1----31-225-11-111123222112--322-12-----222-111------12-1------1---------    0011
13 VERO SPP      ---1--------------------------------------------------------------------------    0011
 4 HOLC LANA     ---1224353133--241--1111----1-------2-----------------------11-1--------------    01
 5 AGRO SPP      --1213324345551231111---321-23122-----11-1----3322323-32133-1221-111-1-1--323423    01
 9 CARE PILU     1213-123--1433345-----------------2-222-1111-------1---------1------------1---1--123    01
 7 DIGI PURP     -2--1111--1--21-2212--1-132132---23212-------1-2-3---1-225----233331-3102-----425    10
 6 HYAC.NONS     32----1-----------------3------------------------------------------2-----23211    11
 8 LUZU PILO     --111---3-35223----1-11222-22121-3112---12-------------3-22243-2122233354353444455    11
14 LYSI NEMO     -------------------------------------------------------------------1----------    11
15 TEUC SCOR     ---------------------------------------------------------------------------2-    11

                 000000000000000000000000000000000000000000000000000000000000000000111111111111111111
                 000000000000000001111111111111111111111111111111111111111111111111000000000000011111
                 001111111111111110000000000000000000000000000001111111111111111111000000000111100011
                   000000111111111000000000000000000111111111111000000000000111100000000011
                   000111000000001100000001111111110000011111111000000000111     0000011
                       0001111     0000111000000111000010000000110011111111     00111

        groups   A       B                C              D              E              F      G   H   I
```

Key

% cover	abundance
0	-
1 - 2	1
3 - 5	2
6 - 20	3
21 - 50	4
> 50	5

Table 2.6. Pilot Study: TWINSPAN classification of seed bank data (litter samples) from Bradford Plan units at Carthamartha Wood.

pattern or gradient in either the soil seed bank or the seeds present in the litter. For the soil samples, nine TWINSPAN groups can be distinguished, although these may be combined to form four groups, A & B; C, D & E; F & G and H & I, as shown in the DECORANA ordination plot (Figure 2.4a.). Groups A, B, C and D all have a low frequency of *Juncus spp.* (mainly *J. effusus*) whereas groups E, F, G, H and I have a higher frequency. *Agrostis spp.* occurs in groups A & B and F, G, H & I more frequently than in groups C, D and E. Groups H & I can be distinguished from groups F & G by higher frequencies of *Epilobium spp.*, *Carex spp.* (mainly *C. pilulifera*) and *Luzula spp.* (mainly *L. pilosa*). Other species, including *Digitalis purpurea*, *Rubus fruticosus* and *Hypericum pulchrum* occur frequently in all groups. On the DECORANA ordination plots showing the canopy stages (Figure 2.4b.) and B-Plan units (Figure 2.4c.), no clear groups can be distinguished. For the litter samples, nine TWINSPAN groups may again be combined to form four groups, A & B; C & D; E and F, G, H & I, as shown in the DECORANA ordination plot (Figure 2.5a.). Groups A, B and E have higher frequencies of *Juncus effusus* than the other groups and groups A, B & D have high frequencies of *Carex pilulifera*. *Holcus lanatus* occurs most abundantly in group B. Groups C & D can be distinguished from group E by the occurrence of *Holcus* and the lower frequency of *Juncus*. Groups F, G, H & I have low frequencies of most species with the exceptions of *Agrostis spp.*, *Digitalis purpurea* and *Luzula pilosa*. In the ordination plots, no groups are distinguishable for the B-Plan units (Figure 2.5c.). There is, however, some correspondence between the TWINSPAN groups the canopy stage groups (Figure 2.5b.). This may be because the presence of seeds in the litter is more immediately influenced by changes in the canopy compared with seeds in the soil.

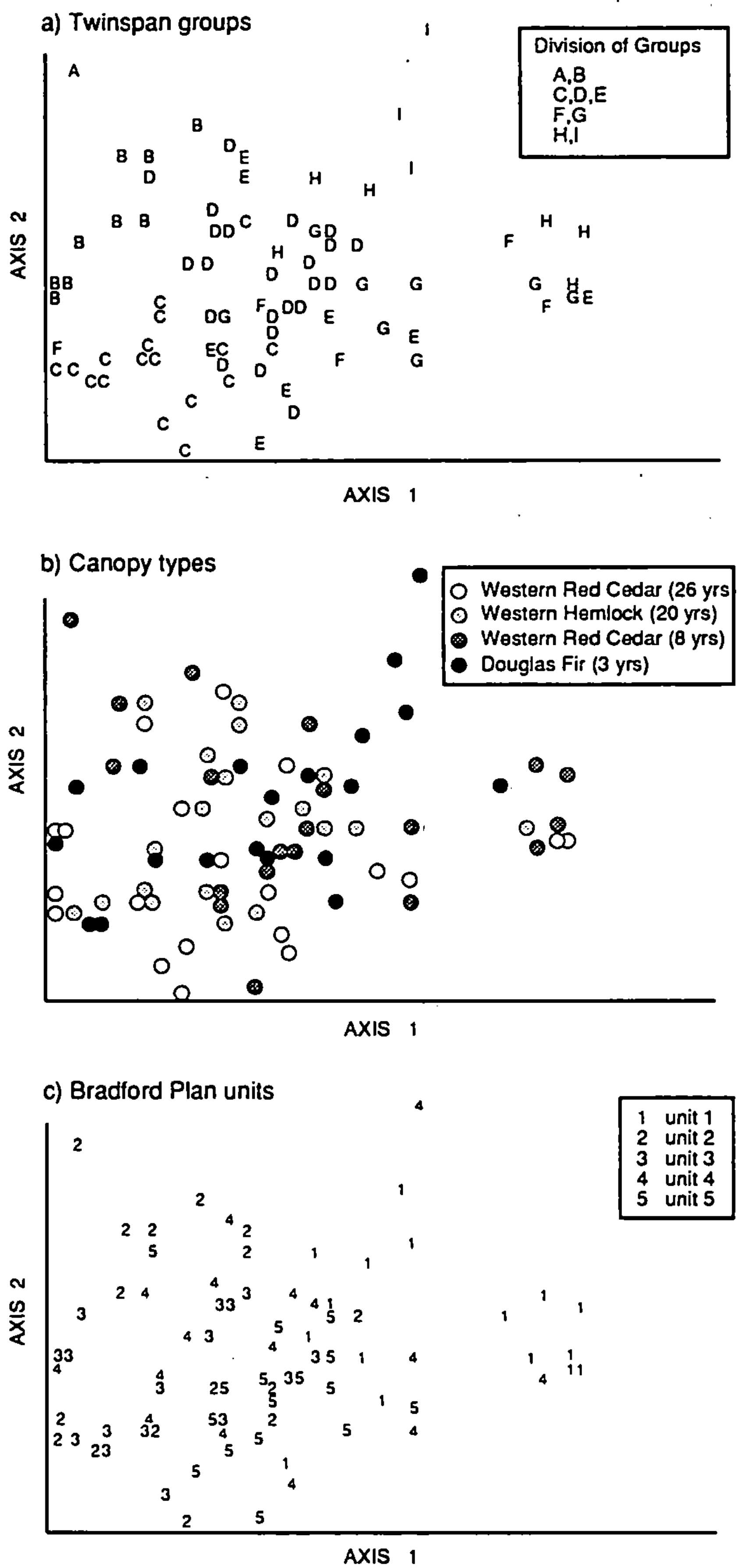


Figure 2.4. DECORANA ordination plots - seed bank survey (soil samples)
Pilot Study : Bradford Plan units at Carthamartha Wood

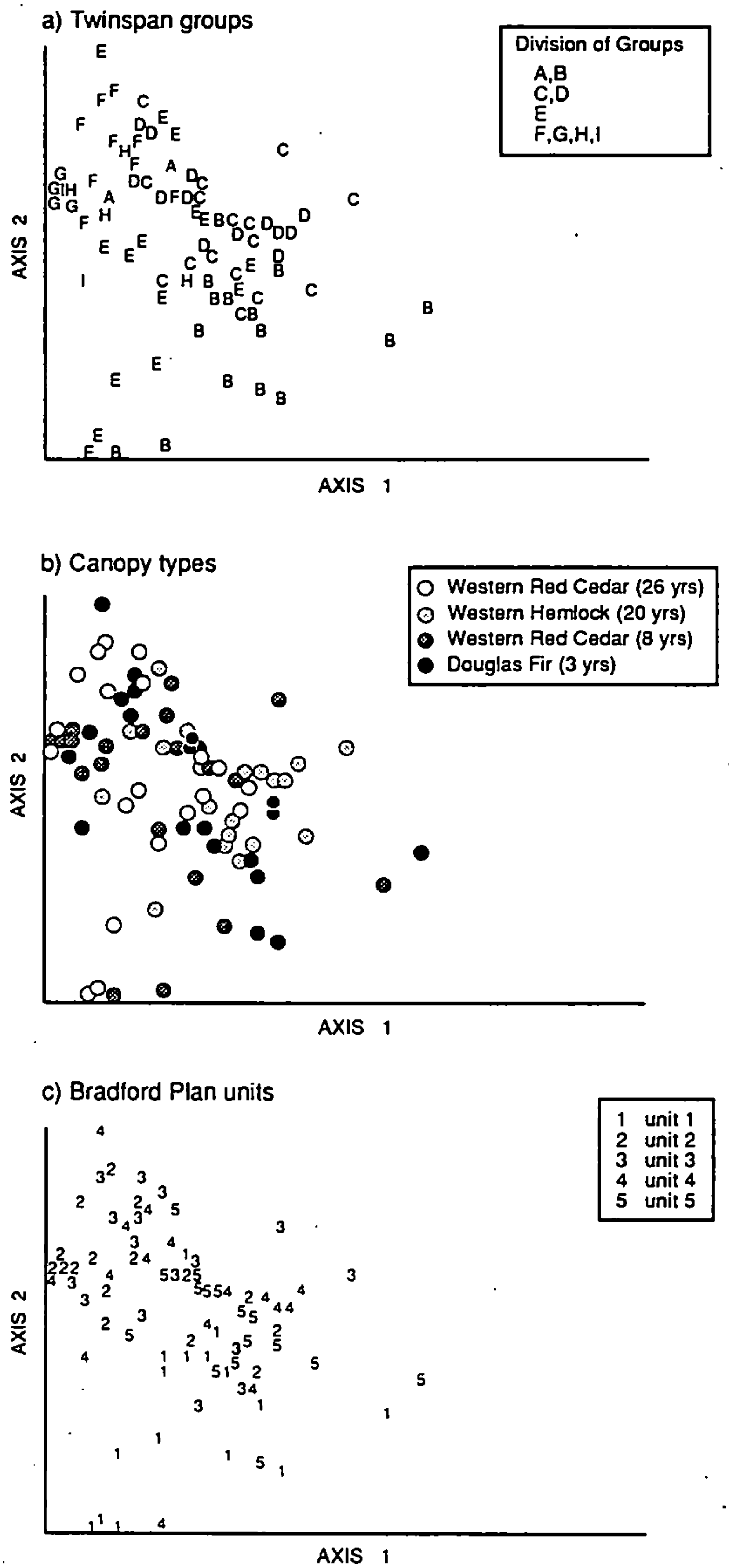


Figure 2.5. DECORANA ordination plots - seed bank survey (litter samples)
Pilot Study : Bradford Plan units at Carthamartha Wood

Statistical analysis of seed bank data

To determine whether differences in seed bank composition of the different canopy stages and/or between units are significant, statistical tests were applied. Before appropriate statistical methods can be used, it is necessary to describe the sampled populations (Benoit et al., 1989). Histograms (Figures 2.6a. and 2.6b.) were used to show the distributions of the numbers of seeds in the soil and litter samples, for the seven most common species. The distributions were all positively skewed. Square root transformations were carried out to normalise the data as much as possible. However, since the distributions were clearly not normal even after transformation (Figures 2.7a. and 2.7b.), the use of parametric statistical methods of analysis was precluded. Instead, the non-parametric Mann-Whitney U-test was used. For this test, no assumptions are made about the characteristics of the distributions of the populations concerned. The only requirement is that the samples are independent. The test was used to make a series of pair-wise comparisons of the mean number of seeds of the different species present in the four canopy stages (six comparisons) and in the five B-Plan units (ten comparisons) for both the soil and litter samples. The results are shown in Figures 2.8. and 2.9. A statistically significant difference between means is an indication that the two samples come from different populations. For three species, *Hypericum pulchrum*, *Juncus effusus* and *Digitalis purpurea*, there are no statistically significant differences in the numbers of seeds present in the different canopy stages in either the soil or the litter samples. There are fewer seeds of *Agrostis* and *Carex spp.* in both the soil and litter samples in the older canopy stages. *Luzula spp.* behaves similarly, but only in the litter samples. There is less *Rubus* in the oldest canopy stages in the soil samples but in the litter there is more *Rubus* in the intermediate canopy stage than in either the oldest or the two younger

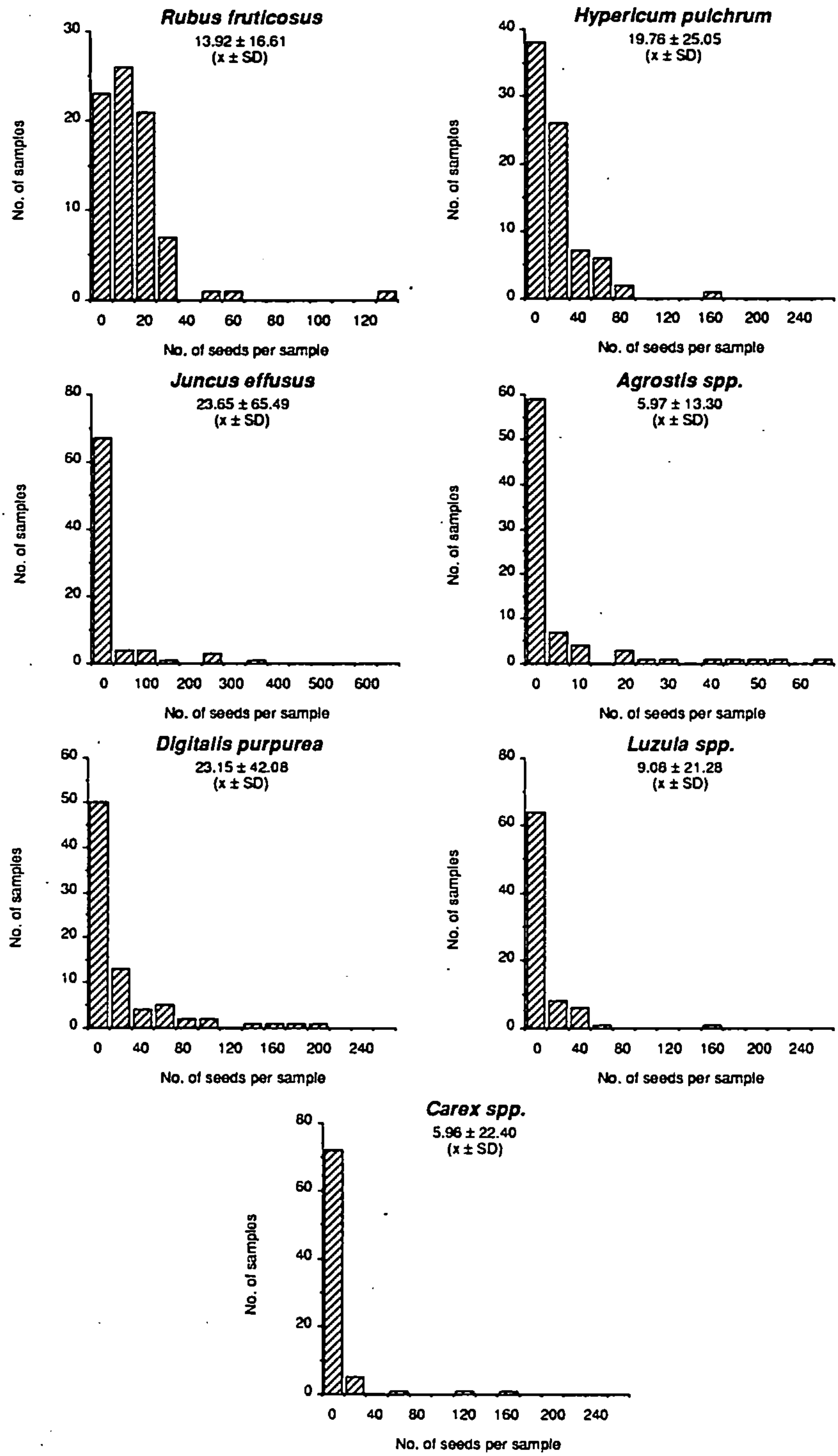


Figure 2.6a Distribution of seeds per sample for the seven most common species in the Pilot Study soil samples.

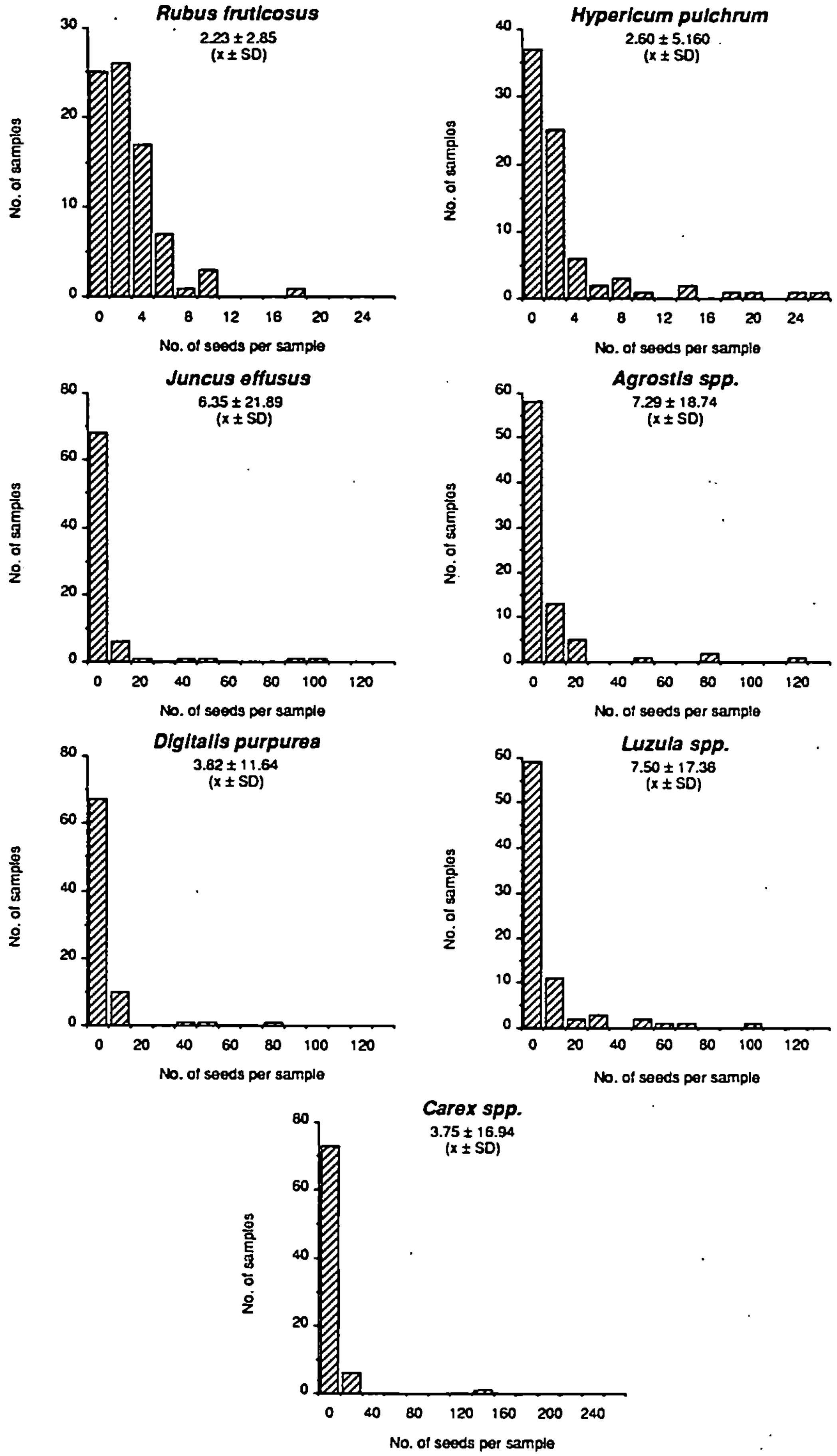


Figure 2.6b Distribution of seeds per sample for the seven most common species in the Pilot Study litter samples.

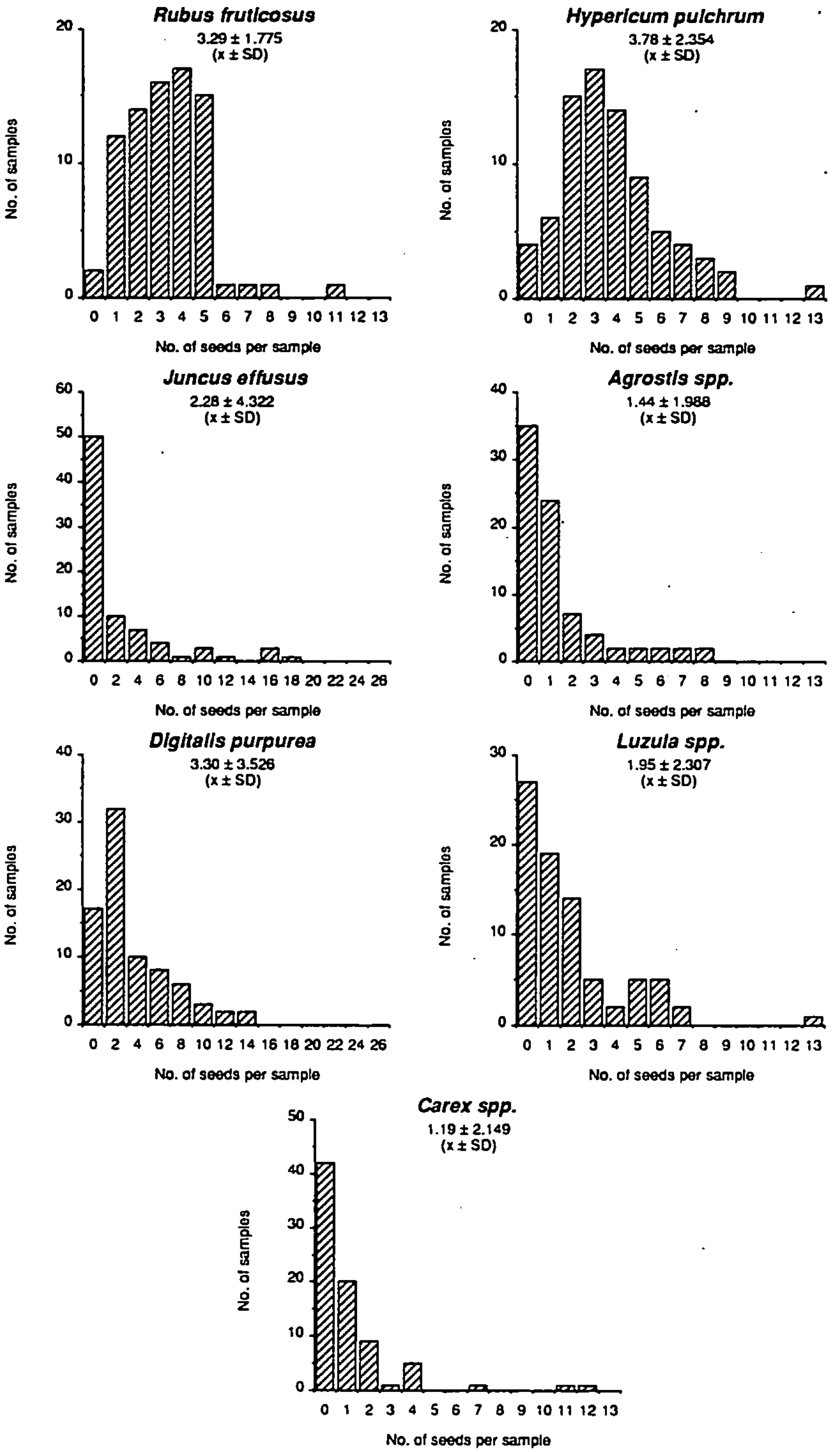


Figure 2.7a Distribution of seeds per sample for the seven most common species in the Pilot Study soil samples after square root transformation.

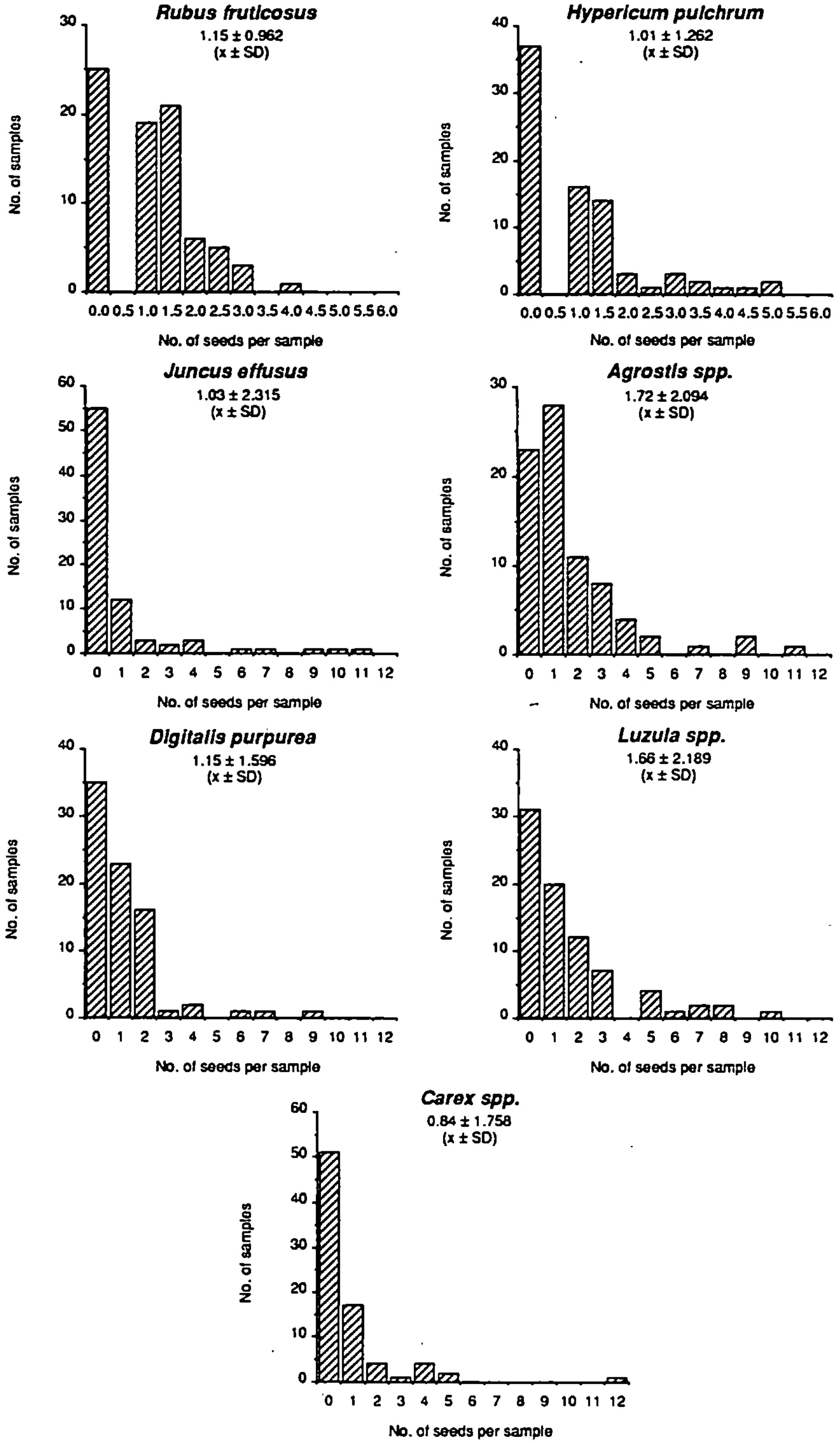


Figure 2.7b Distribution of seeds per sample for the seven most common species in the Pilot Study litter samples after square root transformation.

Soil Samples

Rubus

✱	✱	✱
NS	NS	
NS		

Hypericum

NS	NS	NS
NS	NS	
NS		

Juncus

NS	NS	NS
NS	NS	
NS		

Agrostis

NS	NS	✱
NS	✱	
NS		

Digitalis

NS	NS	NS
NS	NS	
NS		

Luzula

NS	NS	NS
NS	NS	
NS		

Carex

✱	NS	✱
NS	NS	
NS		

Mann-Whitney U-test:

Pairwise comparisons;

1,2	1,3	1,4
2,3	2,4	
3,4		

✱ = significant $P<0.05$
NS = not significant

Species names;
Rubus fruticosus
Hypericum pulchrum
Juncus effusus
Agrostis spp.
Digitalis purpurea
Luzula spp.
Carex spp.

Litter Samples

Rubus

✱	NS	NS
✱	✱	
NS		

Hypericum

NS	NS	NS
NS	NS	
NS		

Juncus

NS	NS	NS
NS	NS	
NS		

Agrostis

NS	NS	NS
NS	✱	
✱		

Digitalis

NS	NS	NS
NS	NS	
NS		

Luzula

NS	NS	NS
NS	✱	
✱		

Carex

NS	NS	✱
NS	NS	
NS		

Figure 2.8. Pilot Study: Results of Mann-Whitney U-tests. Pairwise comparisons of the mean number of seeds present in the four different B-Plan canopy stages for the seven most common species in the soil & litter samples

Soil Samples

Rubus

NS	NS	NS	NS
*	NS	NS	
*	NS		
NS			

Hypericum

NS	NS	NS	*
NS	NS	*	
*	NS		
*			

Juncus

*	*	*	*
NS	NS	NS	
NS	NS		
NS			

Agrostis

NS	*	*	*
NS	NS	NS	
NS	NS		
NS			

Digitalis

*	*	NS	NS
NS	*	NS	
*	NS		
NS			

Luzula

NS	NS	NS	NS
NS	NS	NS	
NS	NS		
NS			

Carex

NS	*	NS	NS
NS	NS	NS	
NS	*		
NS			

Mann-Whitney U-test:

Pairwise comparisons

1,2	1,3	1,4	1,5
2,3	2,4	2,5	
3,4	3,5		
4,5			

* = significant P<0.05
NS = not significant

Species names;

Rubus fruticosus
Hypericum pulchrum
Juncus effusus
Agrostis spp.
Digitalis purpurea
Luzula spp.
Carex spp.

Litter Samples

Rubus

NS	*	NS	NS
NS	NS	NS	
NS	NS		
NS			

Hypericum

NS	NS	NS	NS
NS	NS	*	
NS	*		
NS			

Juncus

*	*	NS	NS
NS	NS	NS	
NS	NS		
NS			

Agrostis

*	*	*	*
NS	NS	*	
NS	NS		
NS			

Digitalis

NS	*	*	NS
NS	NS	NS	
NS	*		
*			

Luzula

NS	NS	NS	NS
NS	NS	*	
NS	NS		
NS			

Carex

NS	*	NS	NS
NS	NS	NS	
*	*		
NS			

Figure 2.9. Pilot Study: Results of Mann-Whitney U-tests. Pairwise comparisons of the mean number of seeds present in the five different Bradford Plan units for the seven most common species in the soil & litter samples

stages. For the between unit comparisons, some differences occur in the numbers of seeds of different species present in different units, but there are few consistent trends. Unit 1 has more *Agrostis* and *Juncus* than any of the other units. The limitations of this analysis and implications for further work are discussed later.

Species composition of seed banks

The bar-charts for the soil samples (Figure 2.10a.) and litter samples (Figure 2.10b.) show how the proportions of the seven most common species in the seed bank differ in the four canopy stages. For most species, there is no pattern in the contribution made to the seed bank composition in the different canopy stages. The only genus to show a consistent trend is *Agrostis*, which is a very minor component of the seed bank in the oldest sub-units but much more abundant in the seed bank of the cleared areas. This applies to both the litter and soil samples.

Numbers of seeds in seed banks

Total seed numbers in both the soil and litter samples differ in the different canopy stages (Tables 2.3. and 2.4.). In the litter samples, there are significantly more seeds in the cleared areas than in any of the other stages. This is due to higher seed inputs for species such as *Digitalis purpurea, Carex spp., Agrostis spp., Holcus lanatus* and *Epilobium spp.*, all of which become more abundant in the ground flora of the cleared areas.

Similarity between ground flora and seed banks

One of the aims of this study was to examine the relationship between the ground flora and seed banks within the different canopy stages associated with the B-Plan

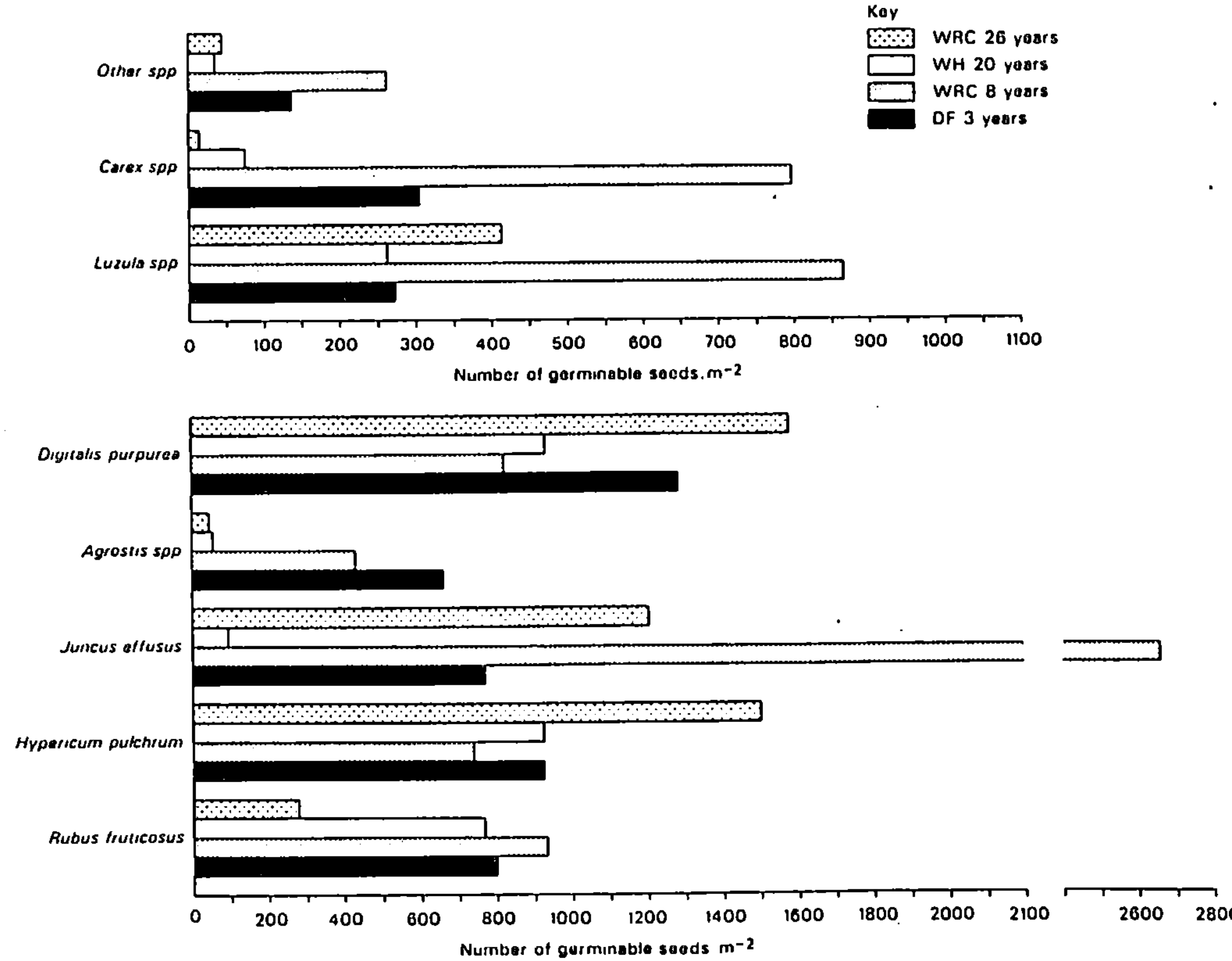


Figure 2.10a. Pilot Study: Species composition of seed banks in Bradford Plan units at Carthamartha Wood (soil samples).

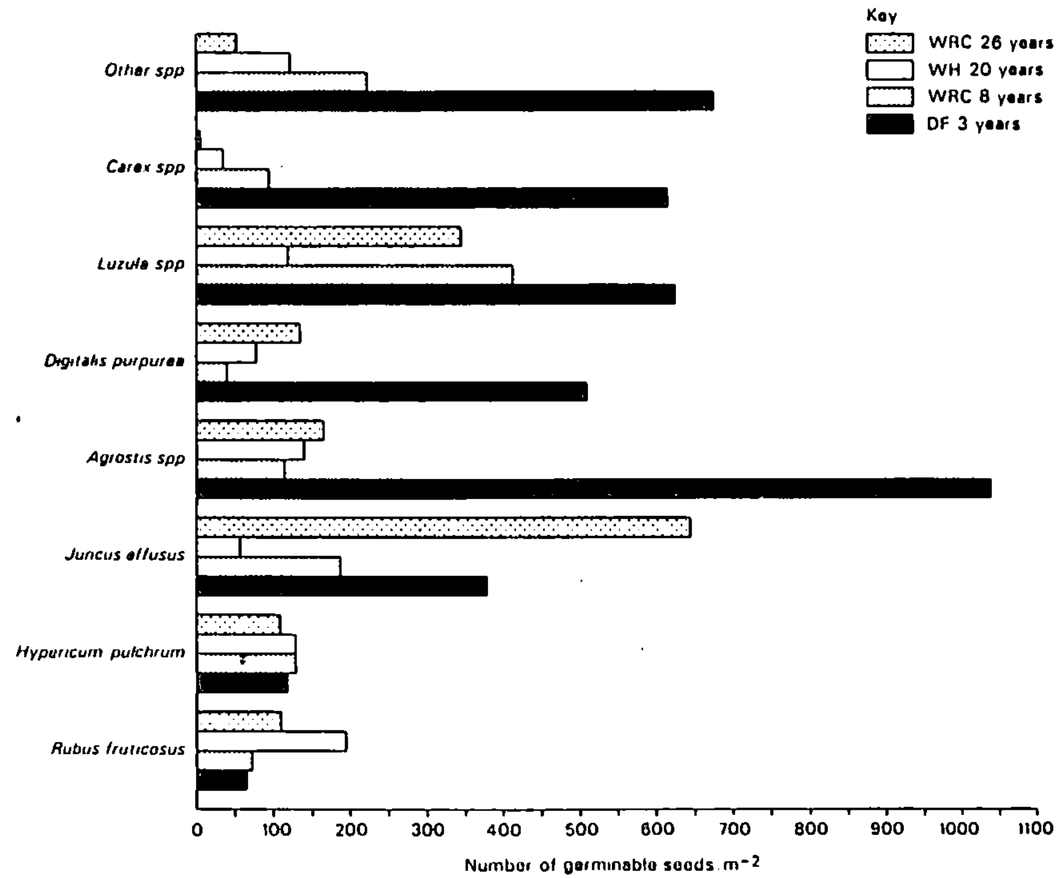


Figure 2.10b. Pilot Study: Species composition of seed banks in Bradford Plan units at Carthamartha Wood (litter samples).

system. The TWINSPAN abundance scores were combined for the two ground flora quadrats and the four corresponding seed samples, both soil and litter, for each of the four canopy stages in each of the five B-Plan units. Czekanowski similarity coefficients were calculated to show the degree of similarity of species composition and abundance between the ground flora and the seed bank. A value of 1 indicates complete similarity, that is two identical sets of species and abundances; whereas a value of 0 is obtained if there are no species in common.

The coefficients for the soil seed bank ranged from a minimum value of 0.000 in the oldest sub-units to a maximum value of 0.593 in the cleared areas (Table 2.7.). This trend results largely from changes in the ground flora, since with the few exceptions mentioned above, the seed banks are not significantly different in the different canopy stages. The differences in the seed banks between the different canopy stages and different units are mostly due to natural heterogeneity. The coefficients for the soil seed bank in the cleared areas were generally higher than for the other canopy stages, but the variation in different samples within any one canopy stage was high. The coefficients for the litter seed bank were more variable than for the soil seed bank. Figure 2.11. shows the distribution of similarity coefficients in the different canopy stages, for both the soil and litter samples.

Tables 2.8a. and 2.8b. show the number of species in the ground flora, the seed bank and the number of species common to both, for the soil and litter samples respectively. A clear trend can be seen, with the number of common species decreasing with increasing canopy age. The species composition of the ground flora and seed bank is therefore most similar after the disturbance caused by felling, as

Table 2.7. Pilot Study: Czekanowski similarity coefficients (C) indicating the degree of similarity in species composition and abundance between the ground flora and seed bank in the four canopy stages.

a. Soil samples

Unit	WRC 26 yrs	WH 20 yrs	WRC 8 yrs	DF 3 yrs
1	0.105	0.263	0.206	0.418
2	0.000	0.264	0.276	0.388
3	0.273	0.316	0.238	0.305
4	0.261	0.295	0.344	0.368
5	0.309	0.243	0.289	0.593

b. Litter samples

Unit	WRC 26 yrs	WH 20 yrs	WRC 8 yrs	DF 3 yrs
1	0.100	0.270	0.082	0.349
2	0.211	0.337	0.161	0.266
3	0.190	0.237	0.029	0.187
4	0.229	0.299	0.338	0.392
5	0.359	0.305	0.173	0.428

$C = 2W/A+B$

Where
A = the sum of species scores in the ground flora.
B = the sum of species scores in the seed bank.
W = the sum of the lesser score of those species which occur in both.

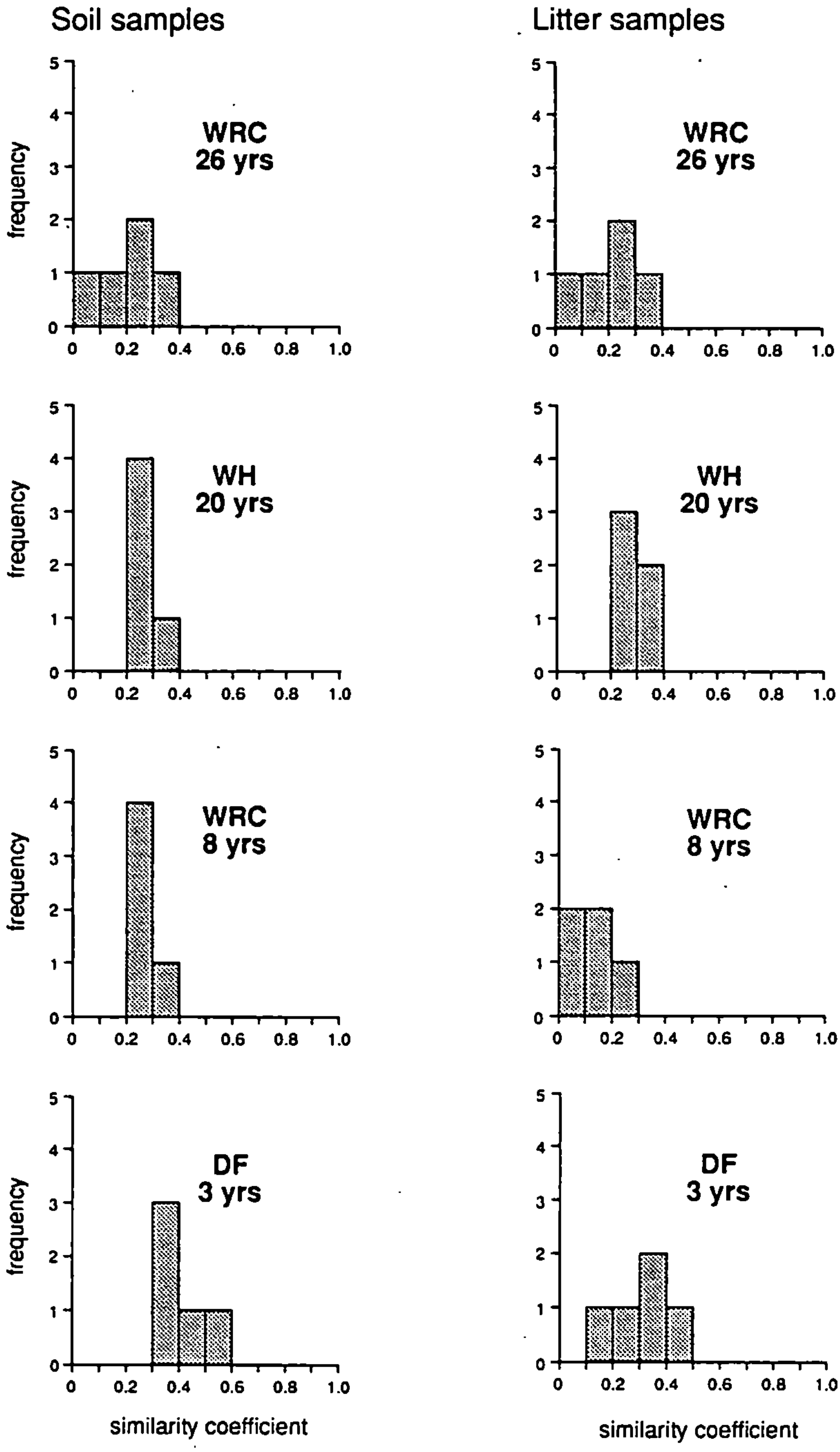


Figure 2.11. Distribution of Czekanowski Similarity Coefficients showing the degree of similarity of species composition & abundance between the ground flora & seed bank in the four different B-plan canopy stages for the Pilot Study soil & litter samples

Table 2.8a. Pilot Study: Similarity in species composition between the seed bank and the ground flora in five Bradford Plan Units at Carthamartha Wood (soil samples).

Unit	Number of species in ground flora	Number of species in seed bank	Number of species in common
WRC 26yrs			
1	2	7	1
2	6	9	0
3	8	7	2
4	2	7	1
5	5	9	3
WH 20yrs			
1	5	7	1
2	7	10	2
3	8	6	3
4	5	7	2
5	6	8	3
WRC 8yrs			
1	5	10	1
2	10	13	6
3	12	9	4
4	10	10	4
5	4	7	1
DF 3yrs			
1	12	10	6
2	11	7	4
3	15	7	5
4	12	9	7
5	6	10	5

Table 2.8b. Pilot Study: Similarity in species composition between the seed bank and the ground flora in five Bradford Plan Units at Carthamartha Wood (litter samples).

Unit	Number of species in ground flora	Number of species in seed bank	Number of species in common
WRC 26yrs			
1	2	9	1
2	6	8	1
3	8	8	2
4	2	6	1
5	5	8	3
WH 20yrs			
1	5	9	1
2	7	11	3
3	8	7	2
4	5	9	2
5	6	10	3
WRC 8yrs			
1	5	9	1
2	10	8	3
3	12	8	3
4	10	10	4
5	4	7	1
DF 3yrs			
1	12	8	5
2	11	7	4
3	15	8	6
4	12	8	7
5	6	9	5

reported in a number of other studies and the ground flora diversity decreases with increasing canopy age.

Effect of chilling on germination

No additional species germinated from the chilled samples compared with the unchilled samples (Table 2.9a. and 2.9b.). The bar-charts show the numbers of the seven most common species which germinated from chilled (Figure 2.12a.) and unchilled samples (Figure 2.12b.). For each of the four canopy stages, a Wilcoxon's Signed-Ranks Test was carried out to compare the number of seeds of each species germinating from the chilled and unchilled samples (Table 2.9c.). No significant differences were found between the sample pairs. The species concerned are common seed bank species in which germination is inhibited by darkness and with the exceptions of *Rubus fruticosus* and *Carex spp.*, chilling is not required to break dormancy (Grime et al. 1988).

Hyacinthoides non-scripta seeds have been shown to have a chilling requirement for germination (Blackman & Rutter, 1954). Seeds of this species germinated from both chilled and unchilled samples indicating that natural chilling of samples in the unheated greenhouse was sufficient to stimulate germination.

2.2.5. Discussion

Since only a relatively small number of samples were collected in this pilot study, care must be taken in the interpretation of the results.

Table 2.9a. Pilot Study: Number of seedlings germinating from chilled soil samples.

Species	WRC 26 yrs	WH 20 yrs	WRC 8 yrs	DF 3 yrs
Agrostis spp.	15	18	31	148
Carex spp.	3	4	198	36
Digitalis purpurea	84	3	11	112
Hypericum pulchrum	168	96	54	98
Juncus effusus/bufonius	334	41	454	252
Luzula spp.	21	10	63	46
Rubus fruticosus	22	34	193	122
Epilobium spp.	-	18	43	2
Holcus lanatus	-	-	3	10
Hyacinthoides non-scripta	-	-	-	2
Veronica montana	-	-	1	-
Total no. of seeds	647	207	1051	828

Table 2.9b. Pilot Study: Number of seedlings germinating from unchilled soil samples.

Species	WRC 26 yrs	WH 20 yrs	WRC 8 yrs	DF 3 yrs
Agrostis spp.	7	14	29	149
Carex spp.	4	2	293	22
Digitalis purpurea	16	2	4	20
Hypericum pulchrum	82	29	34	47
Juncus effusus/bufonius	374	32	864	161
Luzula spp.	13	1	51	28
Rubus fruticosus	28	48	193	94
Epilobium spp.	-	-	14	12
Calluna vulgaris	-	-	-	1
Holcus lanatus	-	-	13	13
Hyacinthoides non-scripta	-	-	1	2
Veronica montana	-	-	8	-
Total no. of seeds	524	128	1504	549

Table 2.9c. Results of Wilcoxon's Signed-Ranks Test for paired (chilled and unchilled) samples

	WRC 26 yrs	WH 20 yrs	WRC 8 yrs	DF 3 yrs
T value	8.00 N.S.	7.00 N.S.	13.00 N.S.	4.00 N.S.

N.S. = not significant

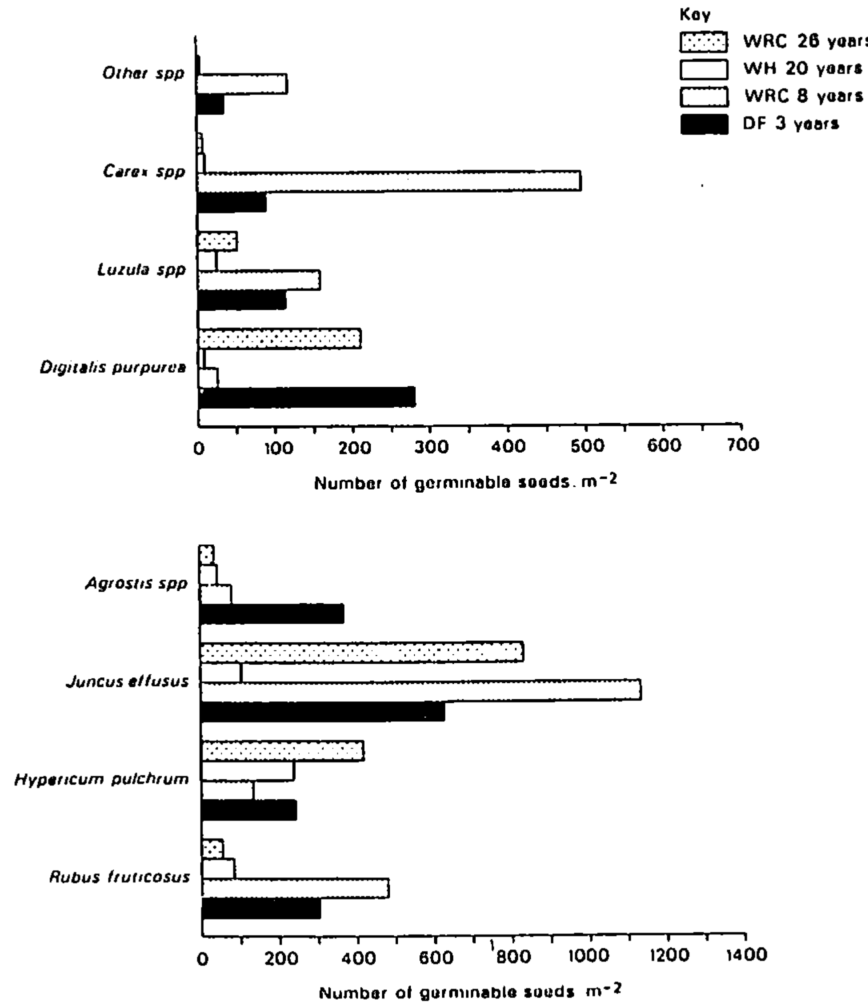


Figure 2.12a. Pilot Study: Germination from chilled soil samples.

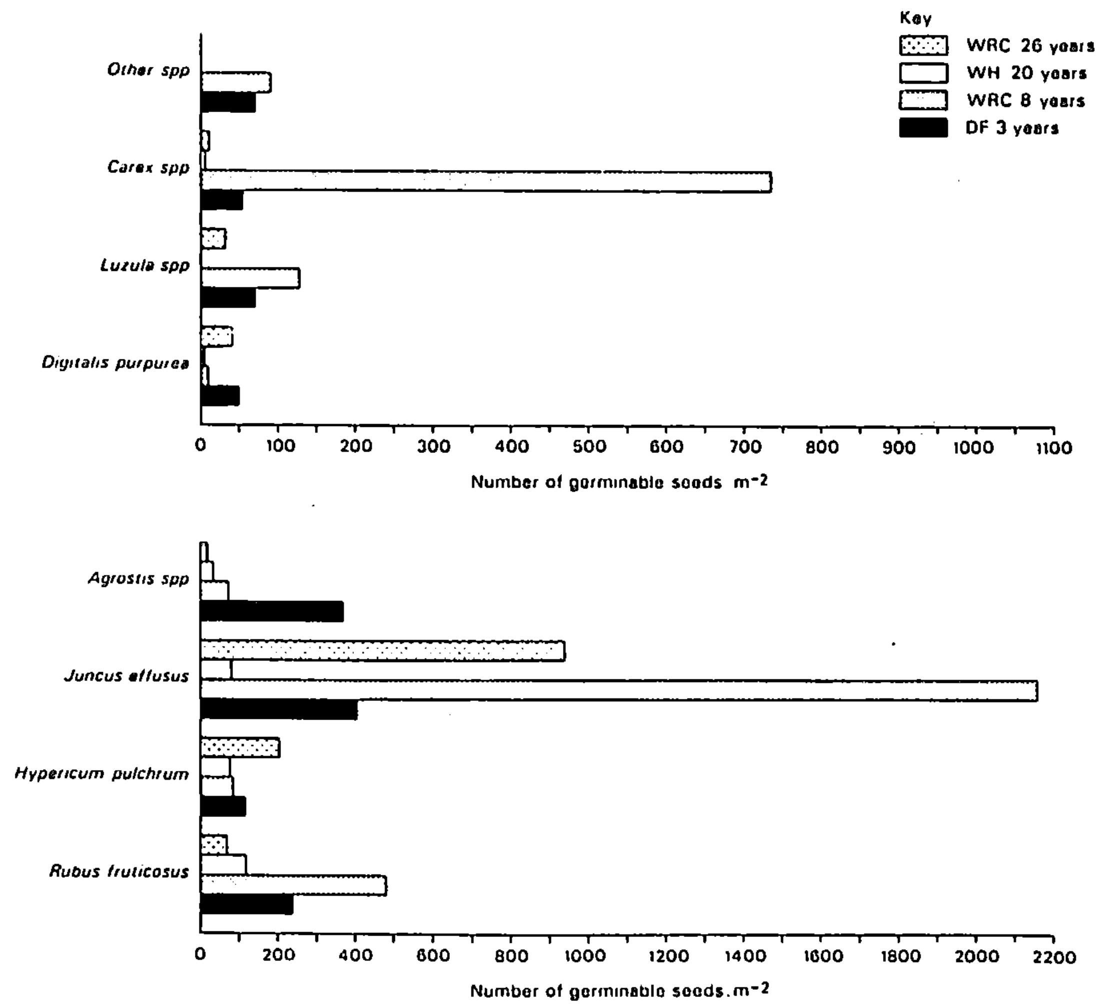


Figure 2.12b. Pilot Study: Germination from unchilled soil samples.

The four groups represent a series of ground flora types of increasing diversity, corresponding to decreasing time since last disturbance and increasing light levels due to more open conditions.

Agrostis (mainly *A. capillaris* and *A. stolonifera*) was the only genus consistently found to have significantly more seeds in the cleared areas, in both the litter and soil samples, than in the older B-Plan sub-units. The higher number of seeds of *Agrostis spp.* in the samples from the cleared areas and the youngest sub-units reflects the increased abundance of *Agrostis spp.* in the vegetation of the cleared areas shown by the ground flora survey. Grasses often become abundant following clear-felling, but decline as the canopy begins to close. Hill & Stevens (1981) found that *Agrostis* seeds had lost their viability after 30-45 years of burial in the soil of upland conifer plantations. The absence of the species in the older sub-units and the inability of the seeds of *Agrostis spp.* to remain viable for long periods of time accounts for the lower frequency of *Agrostis* seeds in the older sub-units.

Another species displaying a similar trend is *Hyacinthoides non-scripta*. Seeds of this species were present only in the cleared areas and the youngest sub-units. The species was not present in the ground flora of the older, more shaded sub-units and the seeds do not persist in the soil. Only a small number of seeds of *Hyacinthoides non-scripta* were found, so it was not included in the statistical analysis.

For most species, seed banks appear to be similar in the different canopy stages. For example, *Digitalis purpurea*, although present only in the vegetation of the cleared areas, is present at high densities in the seed bank of all the canopy stages. The likely reason for the similarity of the seed banks between sub-units is the relatively short period of time that the B-Plan plantings have been established (about 30 years). The ground flora response is immediate, whereas changes in the seed bank take place more slowly. Another reason for lack of differences in the seed bank between sub-units could be the closeness of the different canopy stages within units, permitting seed dispersal between them. The extent to which this occurs will obviously depend on the different abilities of species to disperse their seeds. However, since this apparently does not occur for either *Hyacinthoides*, which has large seeds with poor dispersal ability or *Agrostis*, which has small seeds and a higher potential dispersal ability, it may not be an important factor in seed bank dynamics within the B-Plan units.

2.3. IMPLICATIONS FOR THE RESEARCH PROJECT

2.3.1. Seed Bank and Ground Flora Survey

Collection of soil samples

The method of collection of soil samples in the pilot study was not satisfactory for a number of reasons. The 20 cm x 20 cm (400 cm^2) samples, corresponding with the width of the spade, were too large to fit into the trays. Cutting smaller samples in the field using the spade would be possible but tedious and uniformity of sample size would be less easy to achieve.

Collection of litter samples

Compared with soil samples, the size of litter samples is more difficult to standardize, because different amounts of litter are present at different sampling locations; in the pilot study, the litter layer was generally much deeper in the older sub-units than in the younger stages. It is also difficult to collect litter samples without accidentally including particles of the mineral soil. This may account for the presence of species in litter samples which are absent from the vegetation; for example seeds of *Juncus effusus*, *Agrostis spp.* and *Digitalis purpurea* were recorded in litter samples of the older canopy stages.

Sample location

The regular spacing of sample location within the sub-units is also undesirable for statistical reasons. Alternative methods of sample location are discussed in section 3.2.1.

Choice of sample number and size: Seed bank survey

The high variability in seed numbers between samples is a consequence of the contagious distribution of seeds in the soil. Table 2.10. shows that the variance to mean ratios (Kershaw & Looney, 1985) for the seven most common species are all much greater than 1.

The general formula for the estimation of sample size given by Elliott (1977) was applied to the data. This formula, for the calculation of sample number required to estimate mean population density within prescribed error limits for benthic invertebrates, is relevant since both benthic invertebrates and seeds are dispersed contagiously. This formula ($n = 25 \times \text{variance}/\text{mean}^2$) assumes a normal distribution of the data. The data were not normal, but the formula can still be used to provide a rough estimate of sample number required. Table 2.11. shows that the only

Table 2.10. Pilot Study: Variance:mean ratios for the seven most common species in the seed bank.

Species	Soil samples	Litter samples
Agrostis spp.	29.63	48.17
Carex spp.	84.19	76.52
Digitalis purpurea	76.49	35.47
Hypericum pulchrum	31.76	10.24
Juncus effusus	181.35	75.46
Luzula spp.	49.98	40.18
Rubus fruticosus	19.82	3.66

Variance:mean ratio > 1.00 indicates contagious distribution (Kershaw and Looney, 1985).

Table 2.11. Pilot Study: Number of samples required to estimate mean seed densities in the soil calculated from Elliott's (1977) formula.

Species	Sample number (n)
Agrostis spp.	124
Carex spp.	356
Digitalis purpurea	83
Hypericum pulchrum	40
Juncus effusus	192
Luzula spp.	139
Rubus fruticosus	36
Calluna vulgaris	699
Epilobium spp.	249
Holcus lanatus	296
Hyacinthoides non-scripta	538
Viola riviniana	608

Elliott's formula: $n = 25s^2/x^2$

Where

s^2 = sample variance
x = sample mean

"reasonable" values for n (sample number) were 36, for *Rubus fruticosus* and 40, for *Hypericum pulchrum*. For the other species much higher n values were obtained either because the species occurred infrequently or variation between samples was large. In several cases, n values exceeded 600, for example 699 for *Calluna vulgaris* and 608 for *Viola riviniana*. These results emphasise the importance of taking a large number of small samples when sampling a contagious distribution (Roberts, 1981; Thompson, 1986). However, a compromise is necessary between statistical and practical requirements.

Sampling intensity: Ground flora survey

The sampling intensity of the ground flora survey in the pilot study was insufficient to detect all species present in the ground flora, particularly in the species-rich cleared areas, for example *Epilobium spp.* were not recorded in the survey but were confirmed to be present on a subsequent visit to the site.

2.3.2. Germination Trials

No contaminant species appeared in the control trays in this pilot study. Since the recording was carried out in the early spring, little if any wind-dispersed seed was present. However, control trays are important, particularly when the recording period extends over the summer, when wind-dispersed seed is more abundant and likely to drift into the samples.

Germination began as soon as temperatures started to rise in the spring, confirming that the conditions in the unheated greenhouse provided a suitable germination environment.

As a precaution, the trays were watered with a dilute solution of insecticide. With longer periods of recording, this is necessary at intervals to protect the young seedlings.

2.3.3. Data Analysis

Application of parametric statistical methods to data collected in this pilot study is limited by the requirement for normal distribution of the data. For individual species, the seed abundance data were clearly not normal, even after square root transformations were employed. Another problem is that the non-parametric statistical methods used are only suitable for analysing the distributions of species which occur abundantly in the seed bank. This results in the loss of information concerning species which occur less frequently, yet it is often these species that are of greatest ecological interest.

An important conclusion of the pilot study is that for the analysis of seed bank data, descriptive methods, particularly the use of TWINSPAN (TWo-way INdicator SPecies ANalysis) and DECORANA (DEtrended CORrespondence ANAlysis), are more appropriate and informative than rigorous statistical methods and enable patterns in the data to be discerned.

CHAPTER THREE : TECHNIQUES FOR SEED BANK SAMPLING AND GROUND FLORA SURVEYS; STUDY SITES AND PROJECT DESIGN

3.1. INTRODUCTION

In this chapter, firstly, seed bank sampling and ground flora survey techniques are reviewed. In the following section, the location and description of the study sites is given. Lastly, the project design is outlined, including the procedures adopted for the sampling and survey work and methods of data analysis.

3.2. A REVIEW OF SAMPLING AND SURVEY TECHNIQUES

3.2.1. Seed Bank Surveys

Introduction

One of the problems encountered with seed bank data is the lack of standardization of sampling techniques used in different studies. This makes comparisons between studies difficult. However, it has been shown that there is generally a large amount of variability in both the numbers and species composition of the buried seed present in the soil across a wide range of communities.

Sample collection

In order to estimate the density of seeds of different species present in the seed bank, samples of soil of a known volume must be collected. One method is to use a knife to cut out blocks of soil, which are then removed with a trowel (Olmsted & Curtis, 1947; Marquis, 1975). A more efficient way of collecting samples, used in the majority of seed bank surveys, is the extraction of soil cores with sampling tools. In some circumstances, the use of soil corers may be inappropriate, for example if too many stones or large roots make it difficult to obtain a satisfactory core. Heavy clay soils may also be difficult because the samples get stuck inside the corer.

Sampling intensity

It is an axiom of sampling populations of living organisms that the lower limit of sample size depends on the size of the organisms being studied and their sensitivity to destruction. The sampling tool must not be so small so as to exclude the larger organisms or to destroy a significant proportion of them. Therefore, as pointed out by Bigwood & Inouye (1988), sample size for seed bank studies could theoretically be very small. However, since each sample must be collected and processed separately, which is time-consuming, it is not practical to use very small sample sizes.

As the distribution of seeds in the soil is highly contagious (clumped) and many species occur at low densities, sample variance is large. Estimates of seed densities are imprecise if the number of samples is small (Kershaw & Looney, 1985). As a general principle, it is therefore better to take a large number of small samples rather than a small number of large samples (Roberts, 1981).

Bigwood & Inouye (1988) compared sampling techniques and found that for a given volume of soil sampled, estimates of seed numbers obtained from the largest samples had the widest confidence intervals and were therefore the least precise. They showed that precision could be increased either by making the sample size as small as practical or by taking even smaller samples from large quadrats and bulking them. However, they made the point that although precision may be optimized through the use of appropriate sampling techniques, the accuracy of the estimates is still largely determined by the total volume of soil sampled.

On the basis of the observed variation in seed density between samples, it is possible to calculate the number of samples required to obtain an estimate of seed density within specific error limits. Rabotnov (1958) found that for 100 cm^2 samples, the density estimates of only 7 out of 42 species would be within 15% of their population means with 100 samples. Champness (1949) calculated that to obtain a standard error within 10% of the population mean, using 25 cm^2 samples, 200 samples would be required, even for the most common species. This is clearly too large a sample number for most studies. In any case, care should be taken with the use of such formulae, since it has been shown that they do not always produce a reliable indication of required sample number (Bigwood & Inouye, 1988).

Elliott (1977) has also given a formula, intended for use in determining the sample number required for estimating the population density of benthic invertebrates. Since these are dispersed contagiously in the same way as seeds, the methods are relevant to seed bank studies (Thompson, 1986). Elliott's formula was applied to the data collected in the pilot study (see section 2.3.1.), to provide an indication of the sample number required in the main seed bank survey. Following a study of a pasture seed bank, Thompson (1986), using Elliott's formula, concluded that a minimum of 50 samples would be necessary to produce reliable estimates of the densities of the common seed bank species. Benoit et al. (1989), in their study of the seed bank of

Chenopodium album, reached the similar conclusion that no fewer than 60 samples were required to quantify the seed bank of this abundant weed.

Thompson & Grime (1979), Archibold (1981), Pratt et al. (1984) and Thompson (1986) are examples of studies which have employed a sufficient number of samples (more than 50) to provide a reasonable estimate of the density of seeds of all but the most clumped and/or rare species.

Thompson (1986) pointed out that many studies have used 40 or fewer (often many fewer) samples, for example Champness & Morris (1948), Livingston & Allessio (1968) and Hill & Stevens (1981). The observation that many researchers have taken too few samples has been made by others, for example Major & Pyott (1966) commented that "all investigators have certainly taken too few cores" and Whipple (1978) that "all reports of seed densities in natural vegetation are from too few samples". It follows that many published estimates of seed bank densities are unreliable.

One way of reducing the labour involved with a large number of samples is to use bulked samples. This technique has been used in a number of studies, for example Oosting & Humphreys (1940), Livingston & Allessio (1968) and Brown & Oosterhuis (1981). However, the method is not suitable if the aim is to study small-scale heterogeneity within the seed bank.

Sample distribution

Random sampling is a requirement for the application of conventional statistical methods, for example, Bormann (1953) stated that "the random sample is the only safe basis for statistical calculation". Many studies (Moore & Wein, 1977; Hill & Stevens, 1981) have used random sample cores. However, others have employed systematic sampling such as transects of contiguous cores (Kellman, 1974; Kramer & Johnson, 1987). Contiguous quadrat methods, first introduced by Greig-Smith (1952), have the advantage of simplicity and efficiency over random sampling methods, but there are problems associated with their use, such as chance resonance with natural clustering patterns and problems of spatial autocorrelation. When sampling heterogeneous populations, stratified random sampling is appropriate because separate values for mean seed densities can be calculated for different parts of the sample and the distribution of sampling units is more even (Sampford, 1962). A number of recent studies have considered sampling methods and techniques for determining the spatial distribution of seeds in the soil, termed spatial pattern analysis, for example Benoit et al. (1989), Bigwood & Inouye (1988) and Dessaint et al. (in press).

Timing of sampling

Timing of sampling is important because the seed input and germinability of seeds in the soil varies through the year. Seasonal variation in seed banks has been discussed by Thompson & Grime (1979) and can be related partly to differences in the persistence of seeds of different species in the soil. The seeds of some species can only be found in the soil at particular times of the year, others are present throughout the year. The former are described as having transient seed banks, the latter as persistent (see section 1.5.4.).

The seeds of species with transient seed banks which germinate in the autumn following shedding are absent during the winter and early spring. The seeds of other species with transient seed banks which remain dormant during the winter may be present in the soil but difficult to detect, unless the timing of sampling happens to correspond with the transient "germinable phase" in early spring.

For a many species, germination in the field takes place during the period from May to July, the optimum sampling time for seed bank studies is early spring, from March to April. Sampling earlier than this, while the ground is still frozen after the winter, is not practical.

<u>Depth of sampling</u>

The decision on sampling depth depends on the information required and on the site history. The litter layer may contain many seeds (Strickler & Edgerton, 1976; Moore & Wein, 1977; Pratt et al., 1984). Hill & Stevens (1981) found that in mature conifer plantations, most of the viable seeds were in the top 5 cm of the mineral soil. Short-lived seeds, such as those of *Betula spp.*, *Picea spp.* and *Deschampsia flexuosa* were present mainly in the litter layer. Seeds of most other (long-lived) species were present in the soil and likely to have been there before the conifer litter started to accumulate, for example *Agrostis spp.*, *Calluna vulgaris*, *Carex spp.* and *Juncus spp.*

The way that seeds are distributed in the soil profile may change with time (Darby, 1987). Short-lived seeds are generally concentrated in the litter and upper soil layers since they lose viability before they can reach the lower soil layers. In undisturbed forests, as the canopy closes and the wood ages, the seeds of long-lived, shade-intolerant species will be found increasingly only in the lower layers of the soil profile, as fresh inputs of seed decline and the seeds already present gradually become more deeply buried. The seeds of some species, such as *Agrostis spp.*, lose their viability after several decades and only species with longer-lived seeds, such as *Hypericum pulchrum* and *Digitalis purpurea*, remain. Seeds which are deeply buried may also be more persistent since conditions for survival are more favourable. Seeds of species more tolerant of shade will still accumulate at the soil surface, for example *Rubus fruticosus* and *Betula spp.* These seeds tend to be relatively short-lived and therefore to be found mainly in the upper soil layers.

Estimation of seed numbers in samples

There are various methods for estimating seed numbers in soil samples (Roberts, 1981). Some involve separating the seeds from the soil by washing or flotation, with hand-sorting as a final step. This approach provides an accurate measure of the total number of seeds, but viable seed densities may be overestimated because viable and non-viable seeds cannot be distinguished. For species which are relatively common in the seed bank, viability tests may be carried out and density estimates adjusted. On the other hand, species number may be underestimated if species with similar seeds are present. Extracting seeds from the soil is time consuming, particularly where large numbers of samples are involved, although samples may be stored prior to processing. The technique gives almost 100% recovery with large seeds for example *Rubus fruticosus* and *Rumex spp.* but small seeds are less easily recovered, particularly from soils with a high organic matter content (Roberts, 1981; Gross, in press). Viability tests, such as the tetrazolium test described by Moore (1972), are difficult to carry out with small seeds.

An alternative approach, which has been employed in a large number of studies (Roberts, 1981), is the use of germination methods to provide an estimate of the germinable seeds in the seed bank. The samples are placed in a greenhouse and watered regularly; seedlings are identified at intervals and removed, with periodic disturbance of the soil to promote germination. Seedlings are easier to identify than seeds, but seedlings may be lost, as a result of pests or disease, before they can be identified. Other disadvantages include the amount of greenhouse space required and the delay in obtaining results. Species with specific germination requirements, such as exposure to periods of low temperature, will not be detected if these requirements are not met, causing species number to be underestimated. The seeds of some species germinate rapidly, while others continue to germinate over a long period of time. It is therefore necessary to keep the samples for a long time, two years or more, if a reliable estimate of all the viable seeds present is required. Most studies have shown that, provided conditions are suitable, most germination occurs within the first two months. For example Graber & Thompson (1978) found that in a three year germination trial, most germination (92.7%) took place during the first summer.

Vega & Sierra (1970) kept soil samples of an arable soil for three years and found that 83% of the seedlings appeared in the first year, 16% in the second and 1% in the third. Brown & Oosterhuis (1981) kept soil samples from abandoned coppice for two years. Few seedlings (about 10%) emerged in the second year compared with those in the first year. Although a few species germinated in the second year which had not been recorded in first year, the conclusions drawn from the first year results would not have been different from those derived from two.

Gross (in press) has compared the results of various methods of estimating seed numbers in the soil and suggested that germination methods provide more information about species composition whereas separation methods are more useful for studying variations in seed distribution, particularly of species with easily identifiable seeds.

3.2.2. Ground Flora Surveys

Introduction

Methods for the field description of ground flora in woodlands are not well-documented in the literature. Most description is based on the use of quadrats (Greig-Smith, 1983; Kershaw & Looney, 1985).

Plot location

An important requirement of sample plots is that they are representative of the vegetation type being studied. Subjective siting of plots, in places thought to be representative or "typical", saves time and effort in repetitive recording, although it may not always be possible to recognize "typical" plots. However, for inferential statistical analysis involving probability estimation, plots should ideally be located at random and thus be independent of each other. Where methods of multivariate analysis are being applied there is no such requirement for random data. Such methods are essentially descriptive.

Plot shape and size

Possible plot shapes include squares and circles. Square plots are more convenient to mark out than circular ones and they are also easier to sub-sample (Dawkins & Field, 1978). Large quadrat sizes (100 m^2 or larger) have generally been used for woodland ground flora surveys (Bunce & Shaw, 1973; Westhoff & van der Maarel, 1978).

Plot markers

Pegs or stakes are generally used to mark plots. Ideally they should not be too conspicuous, particularly in areas open to the public, as they may be pulled up. They may also be knocked over accidentally by animals or machinery, so they should be firmly implanted in the ground. It is advisable to mark all four corners of the plot in case any markers are lost. Dawkins & Field (1978) experimented with the use buried metal rods as "invisible" plot markers, relocated using metal detectors. However, their use in woodlands is complicated by the presence of other metal objects in the soil, such as used shotgun cartridges.

Measures of abundance

Some surveys record only whether a species is present. The extra effort required to estimate abundance is often small (Gauch, 1982) and produces more informative data. Abundance is usually measured as cover, an estimate of the area covered by a given species, normally expressed as a percentage of the total area. Visual estimates are subject to personal bias but have the advantage of being quick and easy to carry out. Smartt et al. (1974) have demonstrated that percentage cover estimated subjectively gives a relatively high level of accuracy as well as being rapid to use. Point quadrat methods using pin frames produce more accurate results but recording takes much longer. Sykes et al. (1983) compared visual cover estimates with data obtained from a point-quadrat frame. They found that for most woodland ground flora species, visual estimates fall within a range of plus or minus 10-20% of the mean value. If the same observer repeated the estimate a short time later, the range was reduced to plus or minus 5-15%, suggesting that observer experience can increase the precision of the estimates.

Where data are being analysed using multivariate methods, precise recording of species is not strictly necessary since the results are not affected by differences in the data within a range of plus or minus 0-10% (Hill, 1979b, c; Gauch, 1982).

<u>Seasonal and observer differences</u>

The field season for the recording of vegetation runs from April to August. Data collection may therefore be spread over several months. During this time species may differ in their abundance, conspicuousness and the ease with which they can be identified. For example, vernal species such as *Allium ursinum*, *Anemone nemorosa* and *Ranunculus ficaria* die back by July or August. Another vernal species, *Hyacinthoides non-scripta*, remains conspicuous, as dried stems and fruits are still visible in the late summer. Other species are more commonly recorded in the summer than in the spring, for example, *Eupatorium cannabinum* and *Succisa pratensis*, which have their main period of growth and flowering during the summer.

In comparisons of species lists made by different observers, Kirby et al. (1986) found that most differences arose between records for pairs of similar species, such as *Holcus lanatus* and *H. mollis* or *Luzula campestris* and *L. multiflora*, which can be easily confused when they are not in flower. Generally, differences between observers were less than seasonal differences.

Kirby et al. (1986) concluded that if the aim of the survey is to compare a large number of sites, it would be better to have a team of observers visiting the sites in the same season rather than one observer visiting all the sites over a longer period of time. If the aim is to describe the vegetation at a limited number of sites as fully as possible, it is preferable for a single observer to visit the sites in more than one season (ie. in both spring and summer).

Survey methods and intensities

For statistical purposes, sampling must achieve unbiased representation and distribution. If plots are located randomly, the possibility of personal bias is removed but plots may fall in unsuitable areas. Systematic sampling has the disadvantage that there may be resonance with natural features such as ditches or streams. Stratified random sampling is often used but the basis for stratification has to be decided subjectively. Smartt & Granger (1974), Dawkins & Field (1978) and Kirby (1984) discuss the relative merits of random, stratified random and systematic sampling methods.

As a general rule, the greater the survey intensity, the more complete the description of the vegetation, but a point is reached where the time and effort spent in recording is not worth the gain in additional species recorded. Species-area curves can be calculated to determine the optimum size and number of quadrats, but this method is not suitable where different sites are being compared since a different number of quadrats, or a different quadrat size, would be required at each site and this would be inadmissible on statistical grounds.

3.3. STUDY SITES

3.3.1. Site Selection

Letters were sent to a number of woodland owners and estate managers, explaining the aims and objectives of the research and requesting permission to carry out the survey. Sites were selected from those where permission was granted. One constraint was the limited time and resources available for visiting sites a long distance from Plymouth. The sites selected were mainly lowland sites, all located in south west England (Figure 3.1.). Most of the sites have some areas of ancient woodland, that is, areas which have been wooded continuously since at least 1600 (Peterken, 1977). Most of this ancient woodland was formerly broadleaved and managed as coppice and coppice-with-standards.

The even-aged coniferous forestry practices almost universally applied in Britain to-day are quite unlike former woodland management practices of coppice and coppice-with-standards. The regular phases of light and shade associated with the coppice system are replaced by an extended dark phase which follows closure of the canopy. The ground flora becomes impoverished and this may result in depletion of seed banks, although few studies have been carried out. The results of the investigation carried out by Harris (1986) at the Tavistock Woodlands Estate implied that the opening of the canopy associated with the implementation of the B-Plan forestry system had helped to maintain seed bank and ground flora diversity within a dense-canopied coniferous plantation. However, the seed bank survey was only a small part of the study, which mainly concentrated on changes in the ground flora.

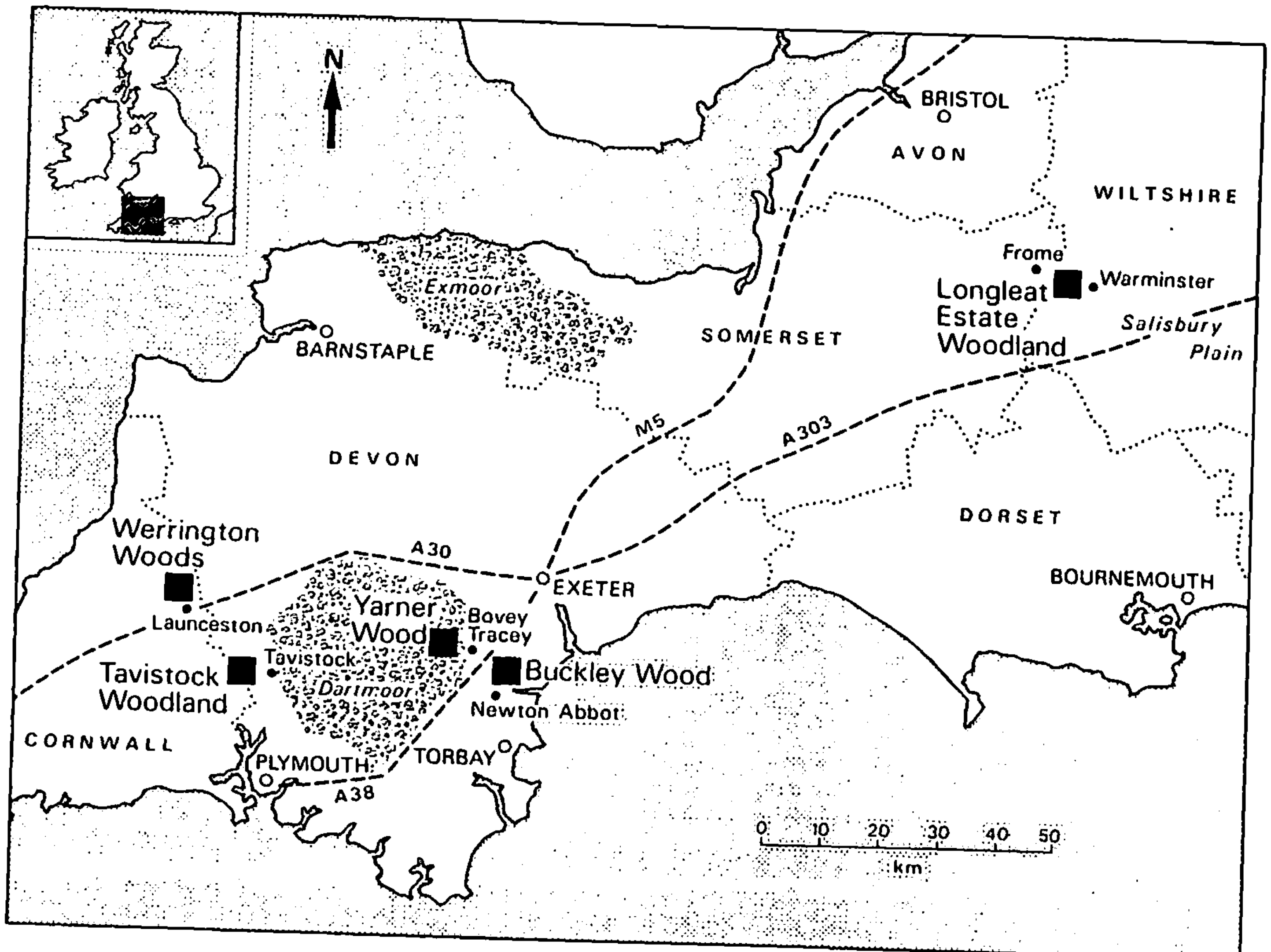


Figure 3.1. Location of study sites.

Consequently, an examination of the differences in both the ground flora and seed bank between individual B-Plan sub-units was considered to be a suitable starting point for this study and was developed into a full-scale pilot study (chapter two).

The procedures followed in the main survey were developed using the information gained from the pilot study. The main survey was carried out in two phases. In the Phase I sampling aimed to investigate seed bank and ground flora diversity associated with two uneven-aged forestry systems: the B-Plan forestry system at Tavistock Woodlands Estate and the mixed conifer plantations on the Longleat Estate. Even-aged stands were also sampled for comparative purposes. The second area of investigation in the Phase I sampling was the effect of coniferisation and neglect on the ground flora and seed banks of coppice woodlands. Two sites were surveyed, the Werrington Woods and Buckley Wood on the Lindridge Estate. The first of these sites is on acid soils and is floristically poor. The second is on basic soils, with a potentially much more diverse ground flora. Ideally the survey should have included some examples of worked coppice but this traditional form of woodland management is no longer practised in south west England.

The study sites were all re-surveyed in the Phase II sampling, which aimed to investigate the distribution of seeds with soil depth. The extent of the survey of the Tavistock Woodlands Estate was reduced in this second phase of the survey, only one B-Plan unit and two coppice plots were surveyed. An additional site, Yarner Wood, was included in the second phase of sampling as an example of an upland acid oakwood.

3.3.2. Site Descriptions

The five study sites are described below:

1. Tavistock Woodlands Estate

The Tavistock Woodlands Estate covers an area of almost 1000 hectares, located in the Tamar and Tavy valleys between Devon and Cornwall (Figure 3.2.). From the dissolution of Tavistock Abbey in 1539 until 1956 the estate was owned by the Russell family who later became the Dukes of Bedford (Harris, 1986). Blanchdown and Grenoven Woods (O. S. grid refs: 420.730 and 416 743; Sheet number 201), were chosen as the main study sites since they have a range of different canopy and management types and are less than 50 km north of Plymouth. These woods were formerly managed as oak coppice-with-standards. Records of woodland management were kept from the 16th century (Harris, 1986). Early records are mainly bills of sale for coppice wood, and from 1700 onwards, records of labouring activities and the sale of timber and wood products. More detailed accounts were kept from the early 1800's onwards, when plantations of native hardwoods and introduced conifers were established in place of the coppice. Species planted include pines (*Pinus sylvestris* and *P. nigra*), larches (*Larix spp.*), spruces (*Picea sitchensis* and *P. abies*) and Douglas fir (*Pseudotsuga menziesii*). Abandoned oak coppice remains in the south west corner of Blanchdown Wood. This area is currently under a cutting scheme as part of a management plan to safeguard a colony of the rare heath fritillary (*Mellicta athalia*) butterfly which has survived in the wood. The species has been observed feeding on *Rubus fruticosus* flowers in clearings between B-Plan units. The larvae

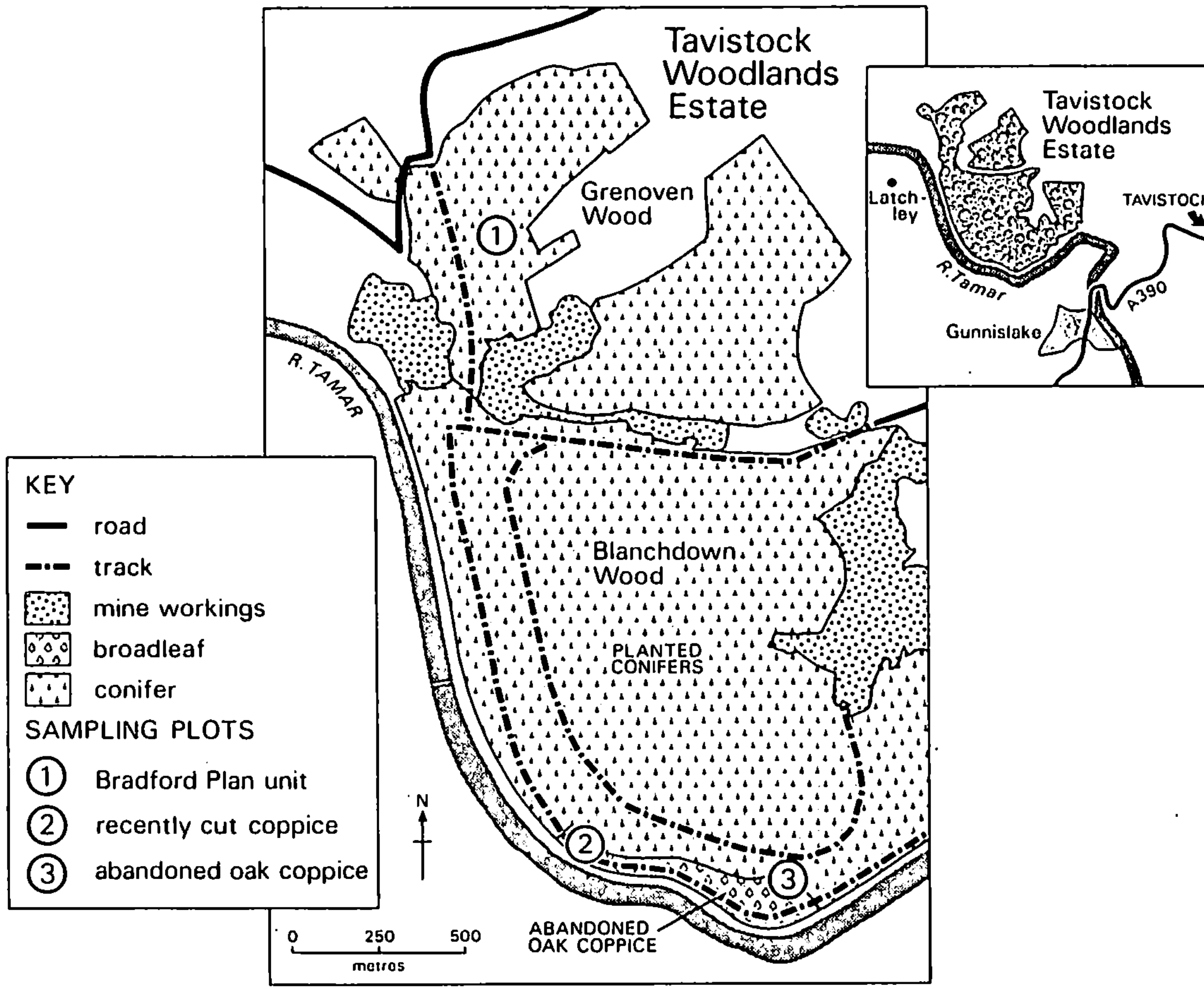


Figure 3.2. Tavistock Woodlands Estate: Location and position of sampling plots in Grenoven and Blanchdown Woods.

feed on the abundant *Melampyrum pratense* growing along the rides and in the relic oak coppice adjoining the units (Warren et al., 1984).

The soils of Blanchdown and Grenoven Woods are mainly acidic brown podsols with a thin surface accumulation of humus. The pH value is fairly low, between 4.0 and 5.5. The area has been affected by mining activities; Blanchdown Wood was the site of the Devon Great Consols Mine, which produced copper and arsenic during the second half of the 19th century.

In 1959, the 6th Earl of Bradford purchased the estate and an attempt was made to convert the existing even-aged conifer stands to a system of commercial forestry based on the continental selection felling system. The system was developed by the late Lord Bradford and his chief forester, Philip Hutt (Hutt & Watkins, 1971; Hutt, 1975) and became known as the Bradford Plan (or Bradford-Hutt) system. The system has been described in section 1.4.1. The steep slopes of the Tamar valley and high rainfall (over 1000 mm/year) make the area unsuitable for clear-fell forestry because of the high soil erosion risk. Continuous cover systems provide protection from leaching and soil erosion (Pryor & Savill, 1986), so they are particularly appropriate in the Tamar valley.

Following the death of the 6th Earl of Bradford in 1981, the estate had to raise money in order to pay death duties. Mature canopy surrounding established B-Plan units was felled in places where extraction was difficult; on steep slopes and where over-mature trees planted in the 1920's were causing damage to young trees during extraction. Felled areas were replanted with Douglas fir. Consequently, the area of the estate under conversion to B-Plan management has been reduced from a proposed 50% to 25%. The disturbance caused by clearing B-Plan sub-units is equivalent to that caused by clear-felling, but on a small scale. Succession of the ground flora occurs within each sub-unit in time, but at any point in time successional stages are represented by the sequence of sub-units within the unit. The aim of the Phase I sampling was to investigate any changes in the seed bank associated with changes in the ground flora resulting from the introduction of B-Plan management in canopies of different ages. Phase I sampling was carried out in May and June 1988 and Phase II sampling in May 1989.

Phase I sampling

The 6 m x 6 m squares of the sampling plots correspond to the B-Plan sub-units. For each sampling plot, the canopy species is indicated. The age of the stand and the year of planting (p.) are also shown. For the Bradford Plan units, the year in which B-Plan was introduced is shown. The figures in brackets indicate the age of the existing canopy at this time.

Bradford Plan units:

1. Douglas fir: 38 years, p. 1950. B-Plan 1961 (11).
2. European larch/Scots pine: 46 years, p. 1942. B-Plan 1961 (19).
3. Norway spruce: 51 years, p. 1937. B-Plan 1961 (24).
4. Douglas fir/Japanese larch: 60 years, p. 1928. B-Plan 1961 (33).

Phase II sampling

1. Norway spruce: 51 years, p. 1937. B-Plan 1961 (24).

2. Cut coppice: cut in March 1986.

3. Abandoned oak coppice: last coppiced around 1916.

2. Werrington Park Estate

The Werrington Park Estate lies north of Launceston in Cornwall (Figure 3.3.). Along with the Tavistock Woodlands Estate, it was originally part of the land belonging to the Tavistock Abbey which passed to the Bedford family at the time of the Reformation. The house was sold to the Williams family in 1882 as a hunting lodge and the estate is still owned by the family. The woodlands are similar to those of Tavistock Woodlands Estate in terms of soils (acidic brown podsols) and previous management (former oak coppice). Detailed records of woodland management operations have been kept. The site is of interest because some of the plantations have reached a greater stage of maturity than those on the Tavistock Woodlands Estate. Rough Hill and Castlehill Plantations (O. S. grid ref: 317 864 and 313 870; Sheet number 201) were chosen as study sites since several different canopy ages and types were present. The stands studied have all been thinned in the last 20 years. The older spruce plantation has been damaged by windthrow and spruce aphid infestation, which has produced an open stand. Phase I sampling was carried out in October 1988 and Phase II sampling in May 1989 and in March 1990.

Phase I and Phase II sampling

Rough Hill Plantation:

1. Sitka spruce: 42 years, p. 1946.

2. Sitka spruce: 28 years, p. 1960.

3. Japanese larch: 42 years, p. 1946.

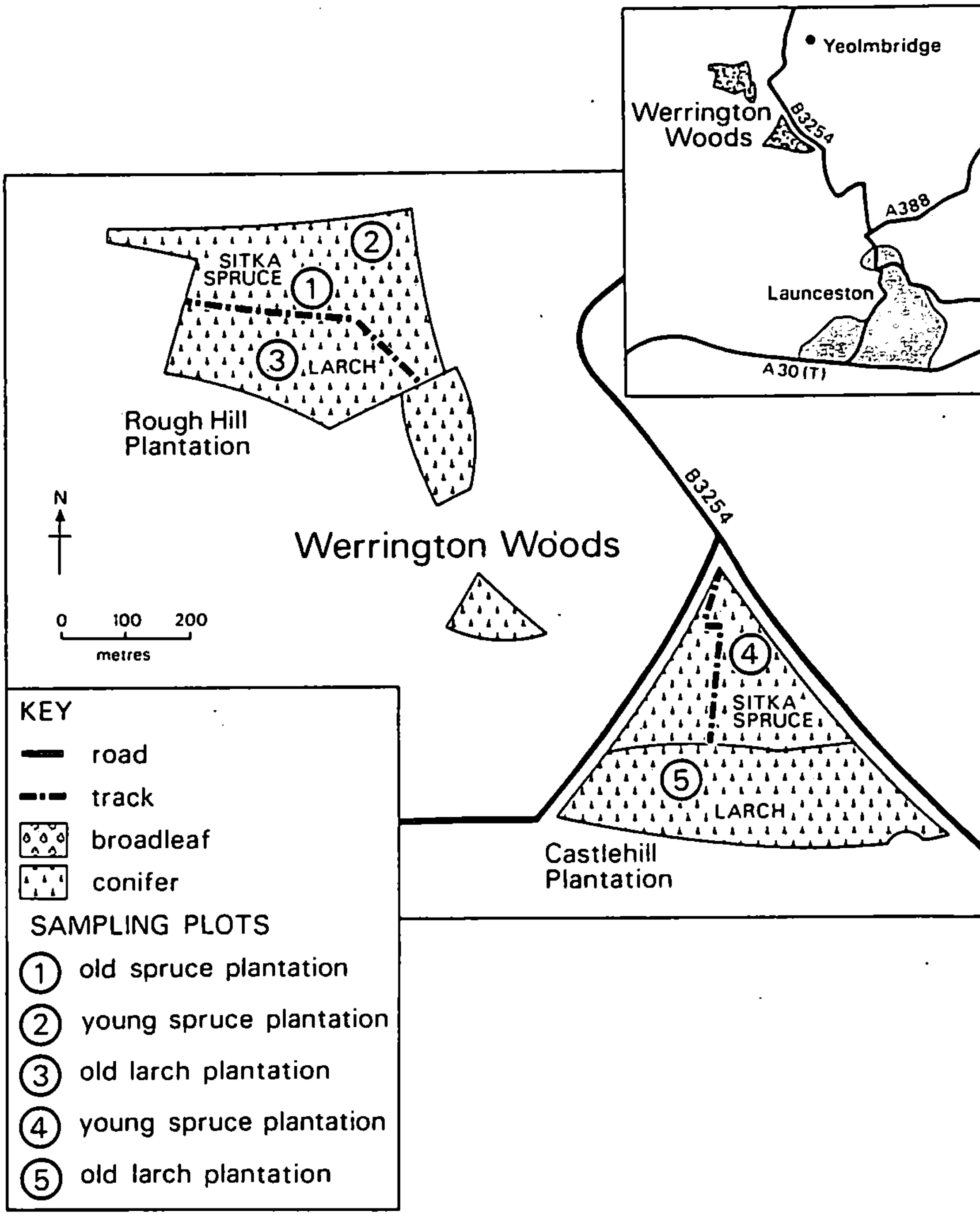


Figure 3.3. Werrington Park Estate: Location and position of sampling plots in Rough Hill and Castlehill Plantations.

Castlehill Plantation:

4. Sitka spruce: 29 years, p. 1959 (see Plate 3.1.).

5. European larch: 53 years, p. 1935 (see Plate 3.2.).

3. Longleat Estate

At the time of the Reformation a man named John Thynne acquired the ruined priory of Longleat in Wiltshire and his descendants have remained in possession of the house. The present owner is the 6th Marquis of Bath; his son, Lord Weymouth lives at the house. The estate, famous for its Safari Park, is located between Warminster and Frome (Figure 3.4.).

The conifers on a large part of the estate are managed using even-aged methods. However, there is an area of 300 hectares (O. S. grid ref: 836 435; Sheet number 183) which provides an example of selection forestry applied to conifers. The system has developed partly as a result of heavy crown thinnings applied to 20-30 year old Japanese larch (*Larix leptolepis*) and Douglas fir (*Pseudotsuga menziesii*) plantations. These thinnings have allowed successful natural regeneration. This is respaced when it is about 2 m tall and herbicide is applied every few years, to control bracken (*Pteridium aquilinum*). Thinnings are generally carried out every five years. Stocking is light at present, however as more age/size classes become established, the canopy will become more complete and weed growth will decline. The diameter increment is high, with an expected "age of exploitation" of 40-50 years (Pryor & Savill, 1986). The soils in this part of the estate are acidic podsols. On a different part of the estate (Blackdog Wood, O. S. grid ref: 826 488; Sheet number 183) there is an oak wood on more basic brown earth soils. Ash and alder are also present in this wood, which

Plate 3.1. Sample Plot 4: Sitka spruce 29 years. Castlehill Plantation on the Werrington Park Estate.

Plate 3.2. Sample Plot 5: European larch 53 years. Castlehill Plantation on the Werrington Park Estate.

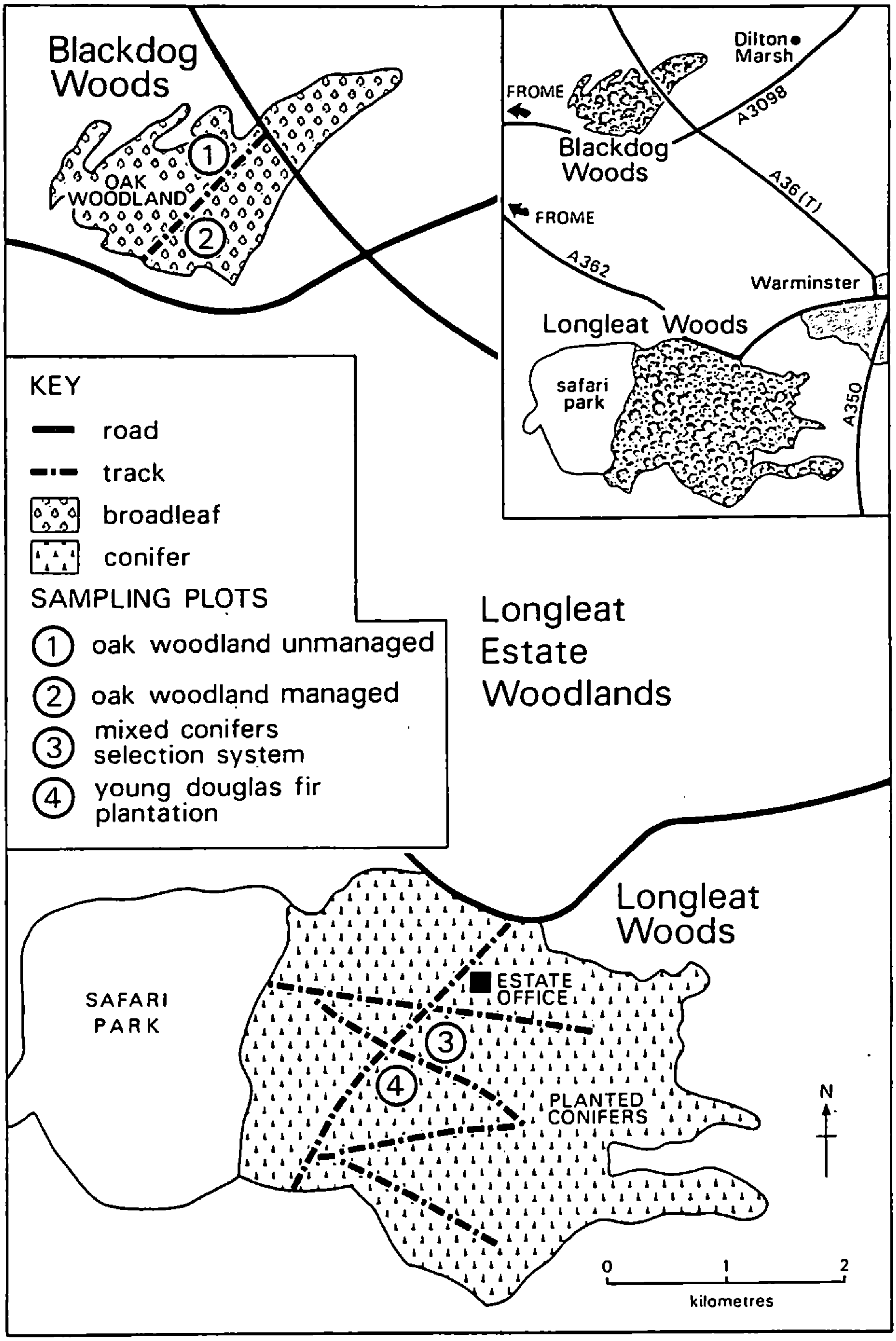


Figure 3.4. Longleat Estate: Location and position of sampling plots in the Longleat Woods and Blackdog Woods.

results from natural regeneration after wartime felling. One stand, the "managed" stand, was thinned and pruned in 1977. All the sampling plots were located in ancient woodland sites, formerly managed as hazel, alder or ash coppice. Phase I sampling was carried out in June and July 1988 and Phase II sampling in June 1989.

Phase I and Phase II sampling

1. Oak woodland: 40 years, "managed" (see Plate 3.3.).
2. Oak woodland: 40 years, "unmanaged" (see Plate 3.4.).
3. Mixed conifers (uneven aged): 18 years (see Plate 3.5.).
4. Douglas fir (even aged): 24 years, p. 1964 (see Plate 3.6.)

4. Lindridge Estate

The Lindridge Estate (O. S. grid ref: 878 746; Sheet number 192), near Newton Abbot in Devon (Figure 3.5.) was sold in 1962 and the woodlands bought by a timber company who proceeded to fell all the usable timber, mainly ash (*Fraxinus excelsior*) and cherry (*Prunus avium*). The company sold part of Buckley Wood in 1965 and this area is currently managed by the Economic Forestry Group (E.F.G.). In 1969 the E.F.G. cleared the remaining trees and the coppice growth from the earlier felling, and planted Douglas fir and hybrid larch (*Larix* x *eurolepis*). The remaining part of Buckley Wood (a semi-natural ancient wood) which was not sold contains abandoned hazel (*Corylus avellana*) coppice with regenerating ash. Although written records have not been kept, this part of the wood has not been managed for at least 70 years. In another section of the wood the remaining large trees (mainly cherry) have been felled and the area replanted with cherry and ash. The soil is shallow and fertile overlying limestone. Since most woodland seed bank surveys have investigated

Plate 3.3. Sample Plot 1: Unmanaged oak stand. Blackdog Wood on the Longleat Estate.

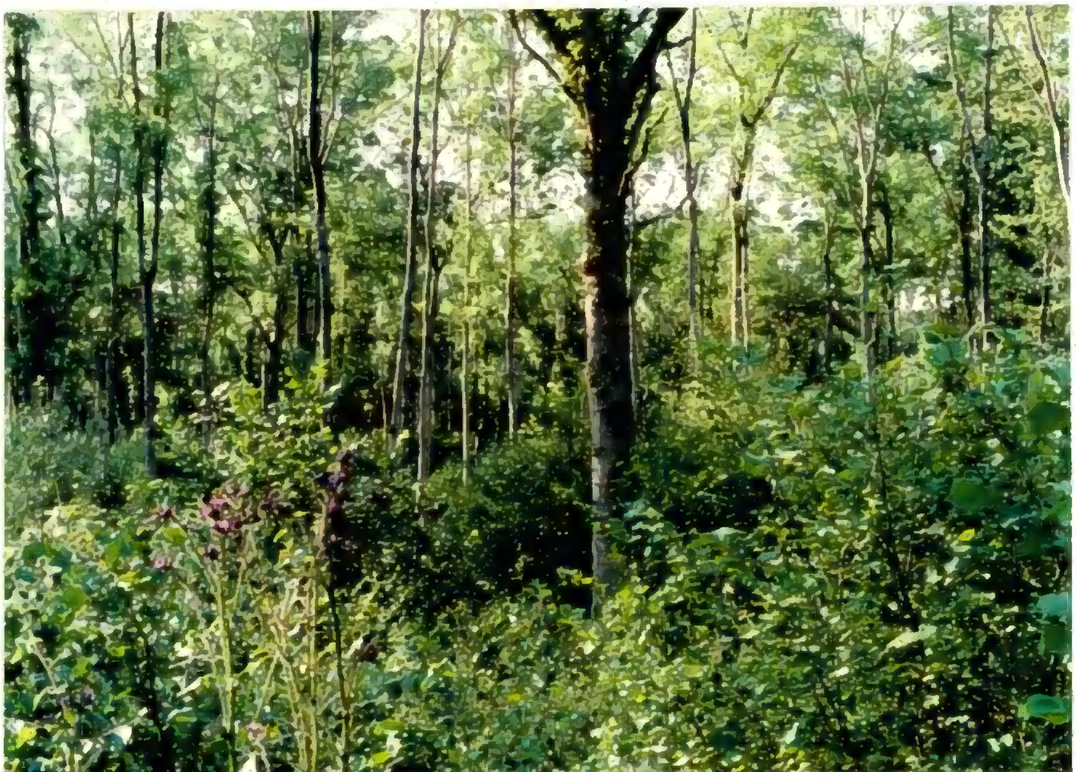


Plate 3.4. Sample Plot 2: Managed oak stand. Blackdog Wood on the Longleat Estate.

Plate 3.5. Sample Plot 3: Uneven-aged conifer stand at the Longleat Estate in Wiltshire.

Plate 3.6. Sample Plot 4: Even-aged conifer stand at the Longleat Estate in Wiltshire.

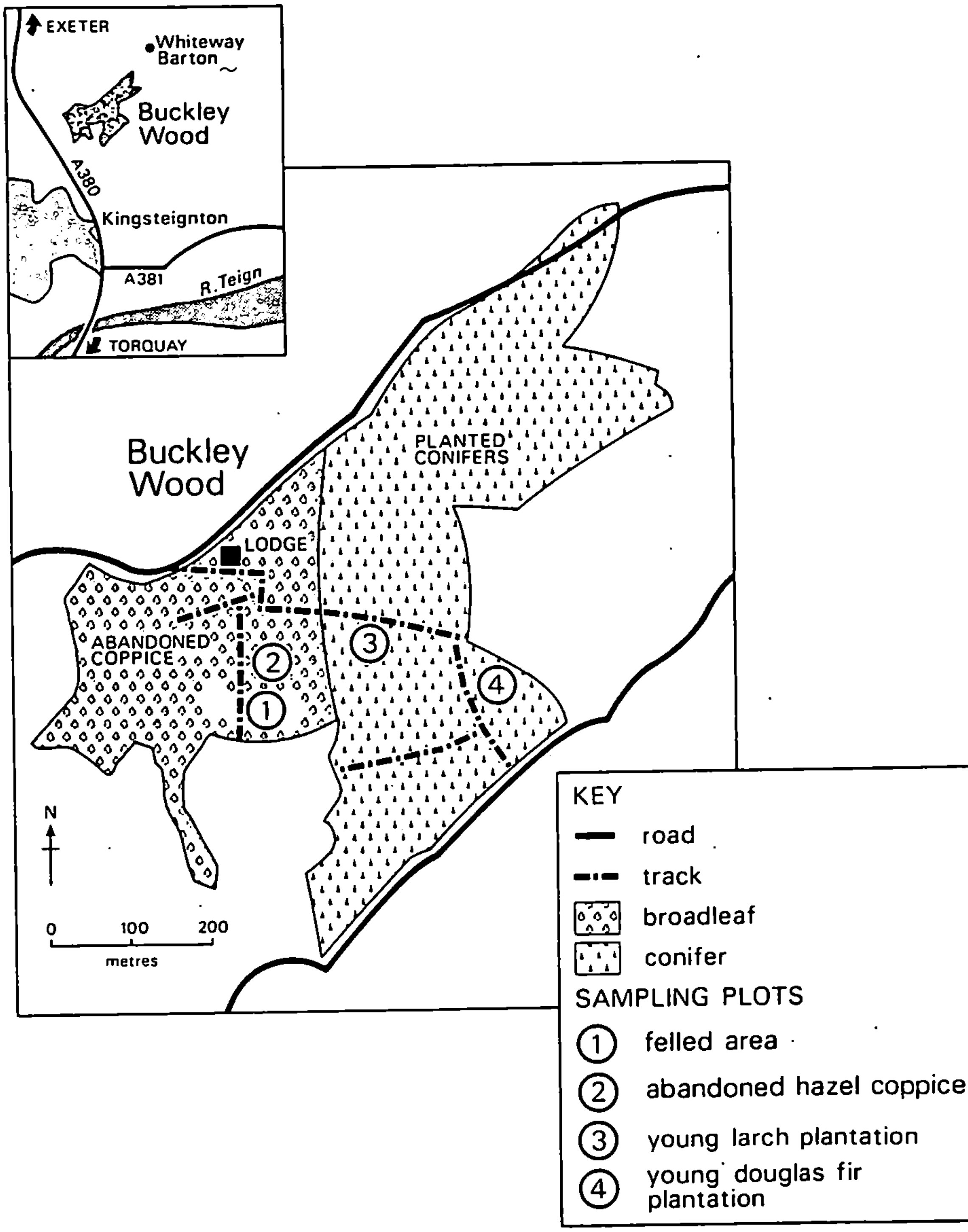


Figure 3.5. Lindridge Estate: Location and position of sampling plots in Buckley Wood.

conifer forests growing on acid soils, for example Hill & Stevens (1981) and Harris (1986), this site was chosen to provide examples of both broadleaf and conifer canopy types on a base-rich soil. Phase I sampling was carried out in April 1989 and Phase II sampling in May and June 1989 and in March 1990.

Phase I and Phase II sampling

1. Felled area: large trees felled between 1962 and 1965, remaining trees cleared in 1987, in order to replant with cherry and ash (see Plate 3.7.).
2. Abandoned hazel coppice: unmanaged for at least 70 years (see Plate 3.8.).
3. Hybrid larch: 20 years, p. 1969.
4. Douglas fir: 20 years, p. 1969.

5. Yarner Wood

This wood (O. S. grid ref: 775 788; Sheet number 191), lies 5 km west of Bovey Tracey in Devon, on the eastern margin of Dartmoor National Park (Figure 3.6.). It is a National Nature Reserve. The soils are mostly infertile acid podsols. The wood covers an area of 150 hectares, mainly of sessile oak (*Quercus petraea*) with some birch (*Betula pendula*) woodland. Much of the oak woodland consists of extensive, closed canopy stands of even-aged trees. The main part of the wood is probably of ancient origin and has been influenced by centuries of coppicing. The oak is mainly abandoned coppice, some of which was singled in the mid-19th century to produce "false" high forest. The age of the trees in this part of the wood is about 150 years. A small block of trees was re-coppiced about 20 years ago, in order to show how traditional management affected the ecology of the wood. The birch woodland results from natural regeneration on abandoned fields. The site is floristically poor; it is a

Plate 3.7. Sample Plot 1: Felled area. Buckley Wood on the Lindridge Estate. Tree-guards protect recently planted trees.

Plate 3.8. Sample Plot 2: Abandoned coppice. Buckley Wood on the Lindridge Estate.

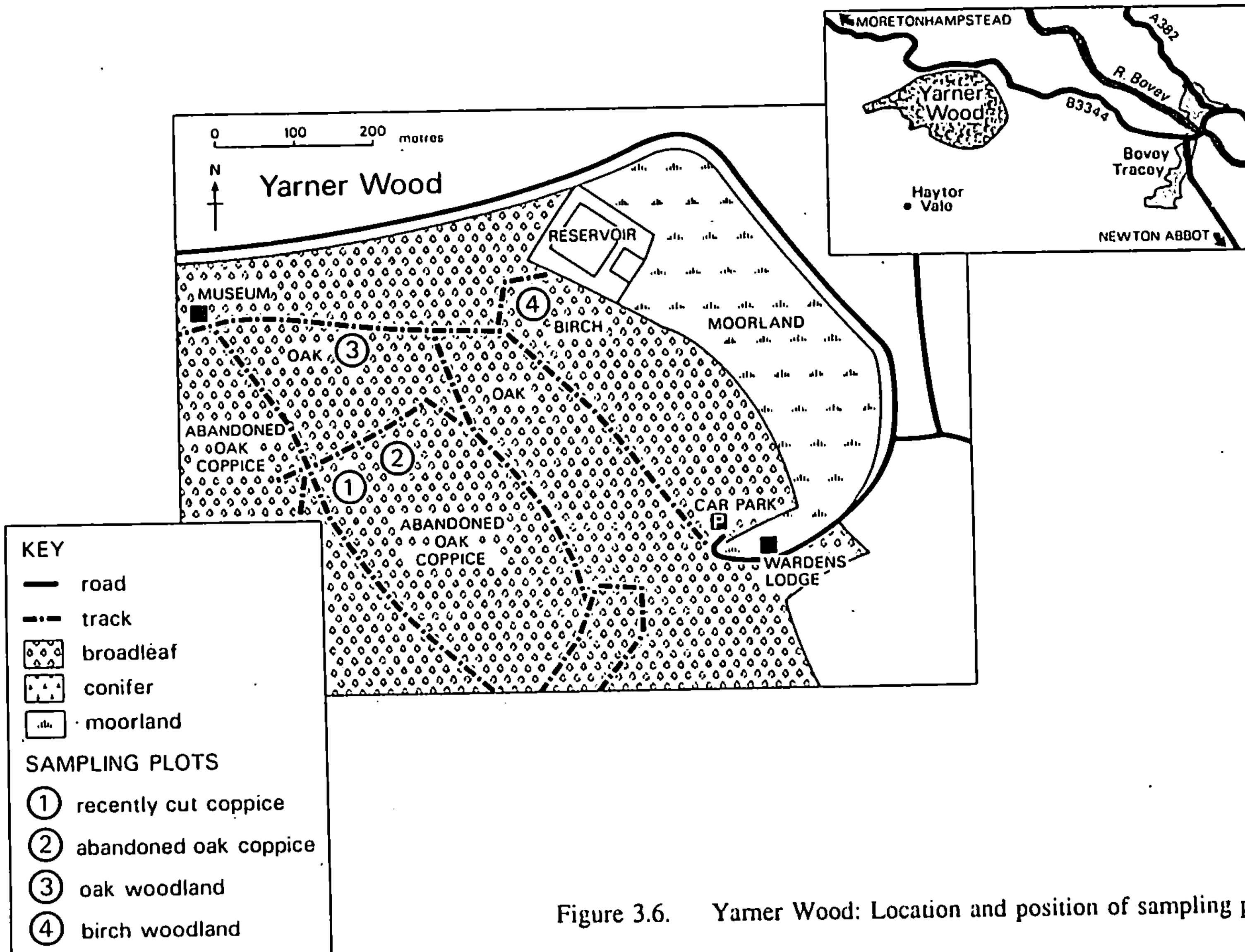


Figure 3.6. Yarner Wood: Location and position of sampling plots.

typical upland site which was included in the survey to provide contrast with the lowland sites. This site was not included in Phase I of the survey; Phase II sampling was carried out in May and June 1989.

Phase II sampling

1. Cut coppice: cut 1969/70.
2. Abandoned oak coppice: coppiced until the early 1900's.
3. Oak woodland: 140 years.
4. Birch woodland: 80-90 years.

3.4. SEED BANK AND GROUND FLORA SURVEY METHODS

The sampling was carried out in two phases which allowed the methods used in the first phase to be refined for the second phase. The basic sampling unit used in the pilot study, a 6 m x 6 m square, was used in both sampling phases. Within each canopy type, the area sampled, subsequently referred to as the sampling plot, consisted of five adjacent 6 m x 6 m squares. The sampling plots were located randomly and marked with wooden stakes which were painted bright yellow to make them easier to locate on subsequent visits.

3.4.1. Phase I Sampling (mainly in 1988)

Seed bank survey

Within each square of the sampling plot, four 1 m^2 quadrats were located using paced random number co-ordinates. Systematic location of the quadrat sampling positions, as in the pilot study, would have been less time consuming. However, systematic sampling is less desirable statistically and there is also the possibility of chance resonance with natural features. After carrying out the ground flora survey, soil and litter samples were collected (Plate 3.9.) from two of the quadrats, at five haphazard positions. The five samples from each quadrat were bulked, so for each plot a total of 50 litter and 50 soil samples were collected, bulked in groups of five to produce 10 litter and 10 soil samples (Figure 3.7.). Bulking reduces the time and effort required in processing the samples and the amount of greenhouse space needed to accommodate them.

Since the sample collection method used in the pilot study was unsatisfactory, various sampling tools were tested. A number of these were rejected on the grounds that they were too heavy to carry or too difficult to use. A simple bulb planting tool (Figure 3.8.) was found to be most suitable. The sharpened edge of the tool allowed it to cut into the ground easily and the hinged opening mechanism facilitated the removal of the soil core. Difficulties with sample collection were only encountered when the soil was very stony or large roots were present.

At each sampling point, a litter sample was collected first, then a soil sample, of the 0-5 cm layer (Figure 3.7.). With a core diameter of 5 cm, the sample size, approximately 20 cm^2, was much smaller (1/10 of the size) than that used in the pilot study, since it was intended to maximize sample number. Bulking of the samples in groups of five produced a final sample (1/2 of the size of that used in the pilot study), which could be spread out in a thin layer in a seed tray. Germination of a high proportion of the buried seeds is more likely if the samples are spread thinly, although

Plate 3.9. The sampling tool is used to collect a soil core.

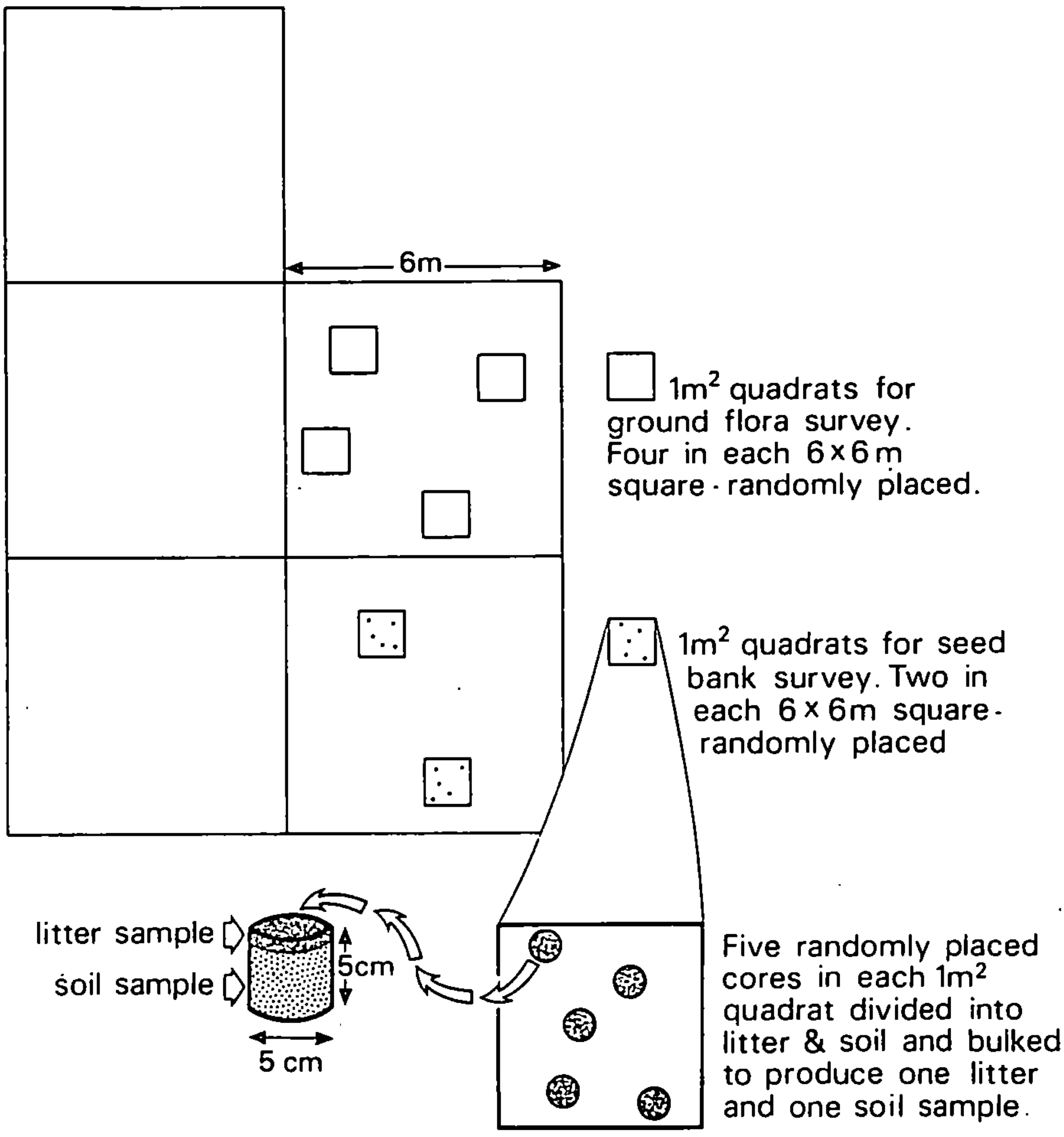


Figure 3.7. Phase I sampling: Location of quadrats and sampling points in a sampling plot.

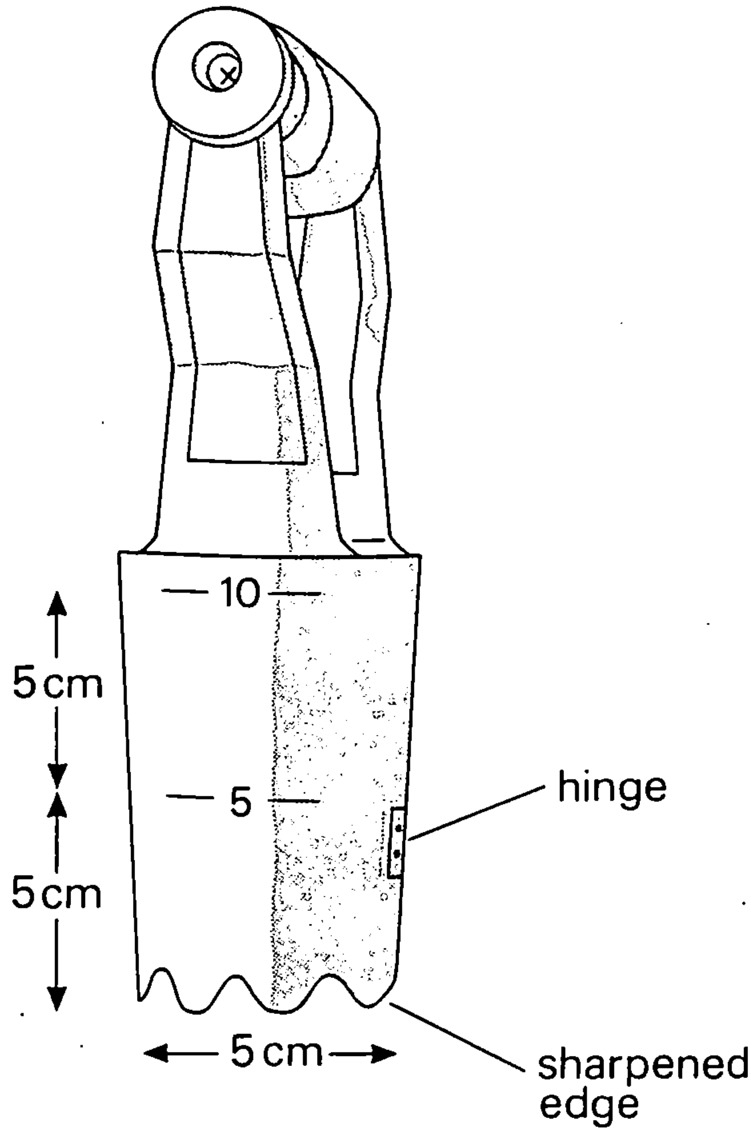


Figure 3.8. Sampling tool used for the collection of soil samples in the Phase I and Phase II surveys.

watering must be frequent to prevent the samples from drying out. Details of the sites and canopy types sampled are given in section 3.3.

Since the sample size was approximately 20 cm^2 (19.64 cm^2) and the sample number 50, the combined surface area of replicate samples for each plot was approximately 1000 cm^2. Coincidentally, this is the area Forcella (1984) found was required to ascertain the number of species present in the seed bank of a cultivated grassland community.

The soil samples were passed through a 1 cm sieve in order to remove stones and roots. Both litter and soil samples were spread thinly on a layer of sand in seed trays. Since greenhouse space was limited, the samples from the Tavistock Woodlands Estate and the Longleat Estate were placed in a shade tunnel. Trays of sand and compost were laid at random in the tunnel to test for wind-borne seed. The shade screen material allowed air to circulate freely whilst restricting the passage of contaminants. Since the litter was light enough to be blown out of the trays, sheets of plastic bird netting were placed over the litter samples (Plate 3.10.). The samples were watered regularly and slug pellets put down at intervals to protect the young seedlings. The samples from the Werrington Woods and Buckley Wood were placed in the unheated greenhouse which was used in the pilot study.

After germination began, the seedlings were counted and removed. The seedlings were identified using Chancellor (1966), Hanf (1974) and Muller (1978). Any which could not be identified at this stage were transferred to pots and grown on, until identification was possible. For this, the keys in Fitter et al. (1974), Rose (1981),

Plate 3.10. Plastic netting is used to prevent the loss of litter from the trays.

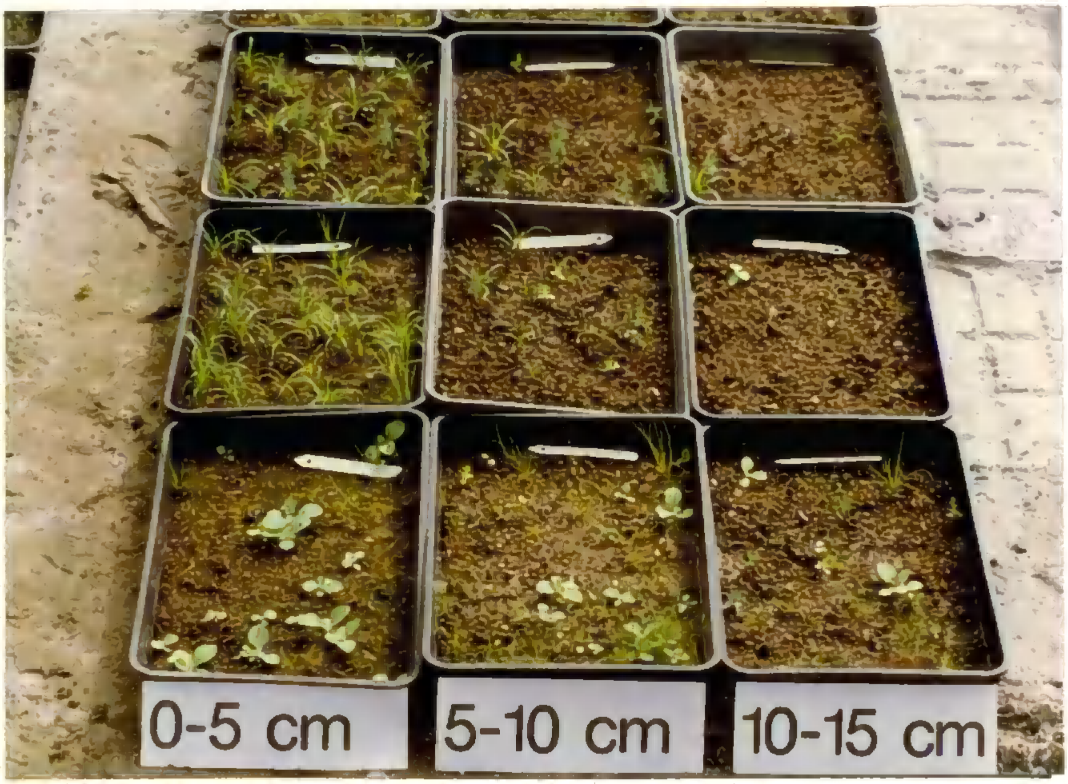


Plate 3.11. Phase II samples on a bed of sand. The samples were kept moist by frequent watering.

Hubbard (1984) and Jermy et al. (1982) were used. Seedlings were also grown on in cases where it was likely that several similar species were present.

Large seeds such as *Ulex gallii* and *Rubus fruticosus* are able to germinate from the bottom of the soil layer in the seed tray but small seeds such as *Calluna vulgaris*, *Digitalis purpurea* and *Juncus spp*. may be inhibited from germinating if they remain at the bottom of the seed tray (Hill & Stevens, 1981). The samples were therefore stirred at intervals. Most germination occurred in the first few weeks, although seeds continued to germinate for several months. The samples were kept for ten to twelve months before they were discarded. No attempt was made to assess the number of ungerminated seeds remaining in the samples, since this would have been too time consuming.

Ground flora survey

The ground flora survey was carried out as far as possible in conjunction with the seed bank survey. Additional visits to sampling plots were made during the late spring and summer where necessary. Since the intensity of the ground flora survey used in the pilot study was found to be inadequate, the number of quadrats was increased. Four 1 m^2 quadrats (two were used in the pilot study) were located using random number co-ordinates within each of the five 6 m x 6 m squares of the sampling plot, making a total of 20 quadrats for each sampling plot.

The percentage cover values of the ground flora species were recorded on duplicated recording sheets, designed for ease of completion in the field. The names of species likely to occur were listed on the sheets beforehand to save time in the field. Tree seedlings and saplings, stump re-growth and woody species such as *Rubus fruticosus* and *Lonicera periclymenum* were included with the ground flora. Mosses and liverworts were recorded in a single category without identification. Other features recorded included the amount of litter, brash, exposed soil and rock. Four 1/2 m^2 quadrats, placed on the ground together, were used instead of a single 1 m^2 quadrat (Figure 3.1.). The four smaller quadrats were easier to carry than one large quadrat and the division of the quadrat into four facilitated cover estimations.

The canopy density affects the vegetation directly; it may be altered as a result of management and varies with the time of year. Canopy measurements are difficult to carry out. One method is to use hemispherical photography, although this requires visits to all plots at a time of seasonal comparability (such as December to February or June to August) and is time consuming. Since exact measurements are not generally necessary, estimates are made using methods such as the leading tree method (Dawkins & Field, 1978). No attempt was made to record canopy densities in this survey.

For each sampling plot, a brief description was made and photographs taken as a visual aid in the later stages of interpretation of the survey data (Plates 3.1. to 3.8.). Since the habitats surrounding the study sites may influence the seed bank, it is important to describe these habitats and to note their distances from the study sites, for example at some of the sites the plantations are bordered by fields.

The presence of species in the seed bank and not in the ground flora can indicate survival of seeds from previous vegetation, but may be due to species being overlooked in the ground flora survey, or being absent at the time the survey was carried out due to seasonal variations. Additional visits to field sites were made where necessary to confirm the presence or absence of species in the ground flora.

Failure of germination tests and modifications to methods

Germination from the samples collected from the Tavistock Woodlands Estate and the Longleat Estate in 1988 was unsatisfactory. A number of factors may have been responsible. Since the trays were in an outdoor tunnel it was not possible to control the temperature and ambient temperatures during the late summer were low. The trays were watered once a day but the thin layer of soil or litter in the trays dried out quickly and the continuous cycle of wetting and drying caused the soil to form a hard crust. Although the soil in the trays was stirred at regular intervals, seeds may have remained dormant under these conditions.

The samples collected in 1989 were placed in the same tunnel but a number of changes were made. The shade netting was covered with a polythene skin so that temperatures and humidities inside the tunnel would be higher. The trays were placed on a bed of sand (Plate 3.11.) which retained moisture and the samples were watered three times a day during hot weather. Satisfactory germination was obtained from the samples in the modified tunnel. Germination in the unheated greenhouse was satisfactory. The panes of glass were treated with a spray-on shading substance and the humidity was controlled.

Estimation of seed densities from the phase I samples

Since the total surface area sampled in each sample plot was 1000 cm^2, seed densities ($seeds.m^{-2}$) were estimated by multiplying the number of seeds germinating from the samples by 10.

3.4.2. Phase II Sampling (mainly in 1989)

In the second year, the ground flora survey was unchanged but the seed bank survey was modified. Litter samples collected in the previous year and as part of the pilot study contained relatively few seeds, partly because of the sparsity of litter at some of the sites, so litter samples were not collected separately. One of the aims of this second phase of sampling was to investigate the depth distribution of seeds in the soil. The sampling tool was used to collect five soil cores, as in the Phase I sampling, but from just one 1 m^2 quadrat, located randomly within each of the five 6 m x 6 m squares of the sampling plots. In this phase, three soil layers (0-5 cm, 5-10 cm and 10-15 cm) were sampled and cores from the separate layers bulked. A total of 75 cores was collected from each sampling plot, bulked in groups of five to produce 15 samples, five at each depth (Figure 3.9.). The reduction in the total number of samples collected from each sample plot, compared with the phase I sampling, was due to constraints of time and space to carry out the germination tests. Sampling was carried out at all the sites sampled in the previous year and at one additional site. Details of the sites and canopy types sampled are given in section 3.3. All the phase II samples were placed in the modified shade tunnel. Since the total surface area sampled in each sample plot was 500 cm^2, seed densities ($seeds.m^{-2}$) were estimated by multiplying the number of seeds germinating from the samples by 20.

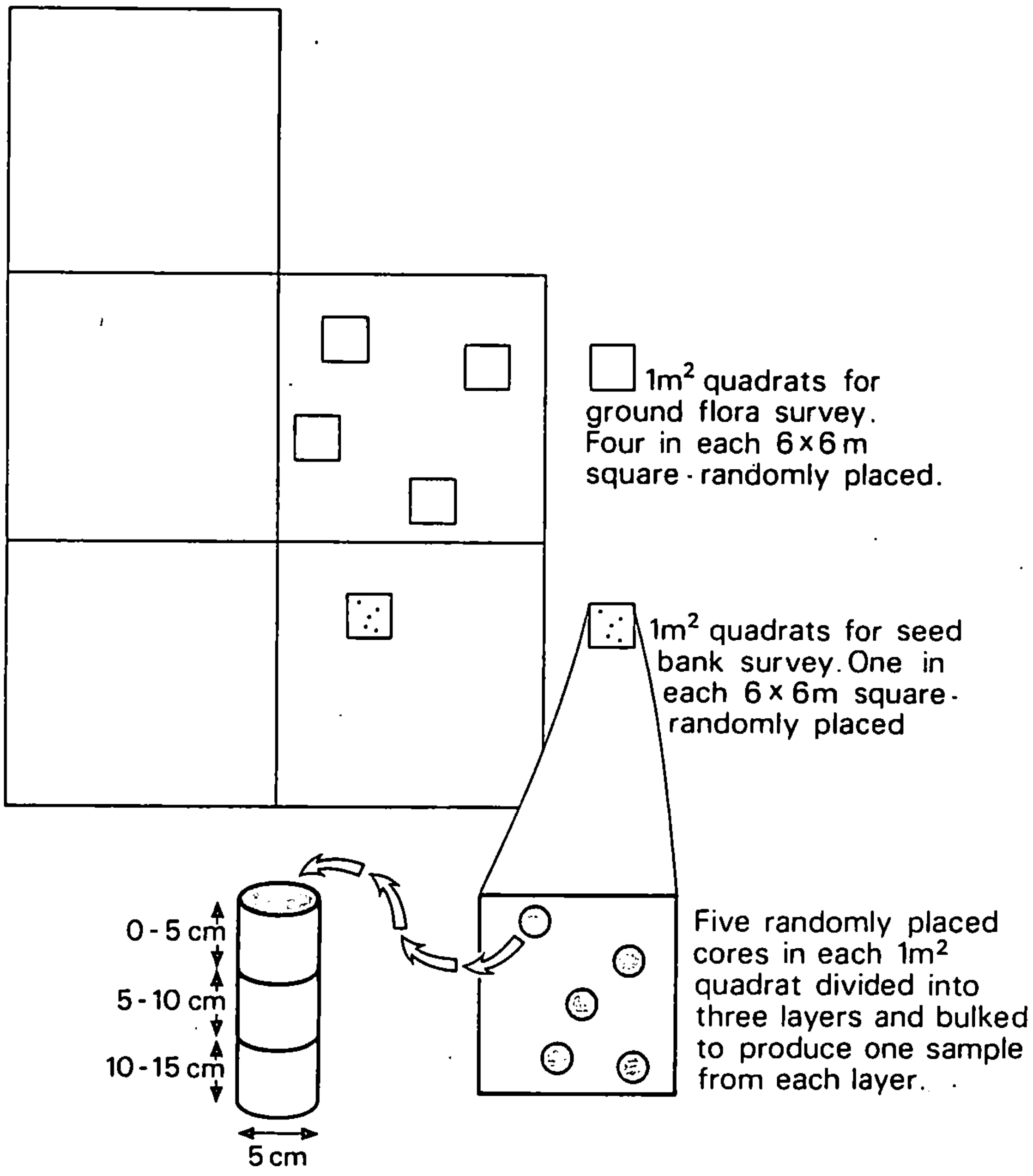


Figure 3.9. Phase II sampling: Location of quadrats and sampling points in a sampling plot.

3.4.3. Seed Rain Survey

The aim of the seed rain survey was to measure seed inputs beneath a range of canopy types and to compare the estimated density of seeds in the seed rain with that in the soil.

Seed trays were filled with a mixture of bark and peat on a layer of sand. The flakes of bark were used to give some extra weight to the peat to prevent it from blowing away. Single trays were positioned in three of the five 6 m x 6 m squares at each of the sampling plots (Figure 3.10.). The trays were sunk into the ground, so that the peat was level with the soil surface. The trays were put out in May 1989 and collected in November 1989 (Plate 3.12.). They were placed in the unheated greenhouse and germination recorded in spring 1990. The seed rain survey was carried out at Tavistock Woodlands Estate, the Werrington Woods and Buckley Wood, on the Lindridge Estate. Since the total surface area for seed trapping was 2415 cm^2 in each sampling plot, seed rain densities ($seeds.m^{-2}$) were estimated by multiplying the number of seeds trapped by 4.

3.4.4. Ride Survey

The aim of the ride survey was to assess whether gradients of seed density of particular species occurred due to the presence of the ride and to examine the correspondence between species composition in the ground flora and seed bank.

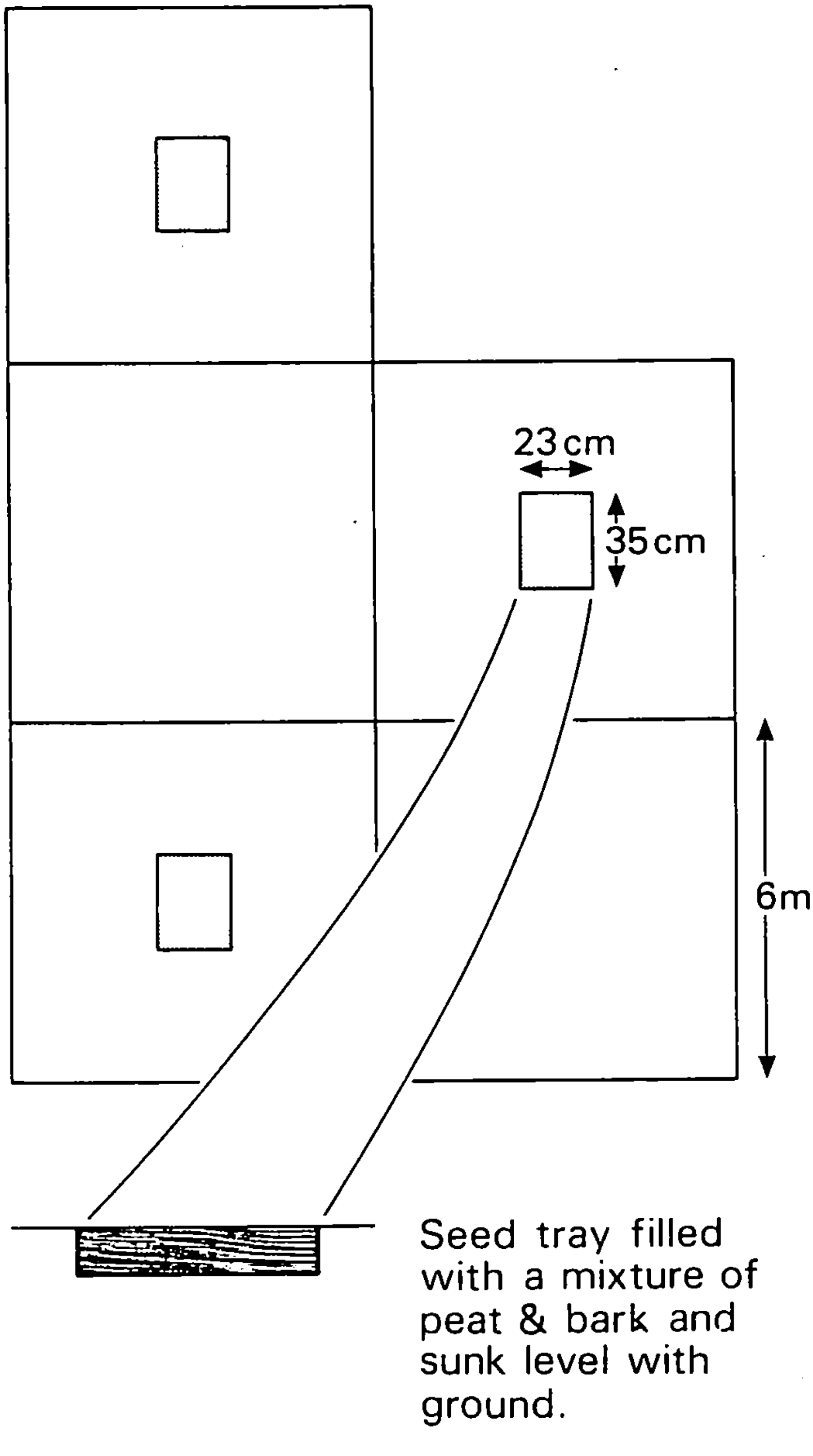


Figure 3.10. Seed rain survey: Positions of seed trays in a sampling plot.

Plate 3.12. Seed rain survey: Tray just before collection.

The ride survey was carried out in July and August 1989. Four rides were surveyed, two at the Werrington Park Estate and one at the Tavistock Woodlands and Lindridge Estates. Sampling was carried out along a transect which traversed the ride (Figure 3.11.).

The 0-5 and 5-10 cm soil layers were sampled where possible, but at Buckley Wood, on the Lindridge Estate, the material used in the construction of the ride prevented sampling at the lower depth. The five cores taken from each sampling point were bulked, to produce a single sample from each layer. The number of samples in each transect varied with the width of the ride. Two samples were collected from beneath the canopy of the plantation on both sides of the ride, one sample from each side of the ride (or two samples if the ride edge was wide) and two samples from the ride itself. The ground flora at each sampling point was recorded in two 1 m^2 quadrats placed on either side of the transect (Figure 3.11.).

The soil samples were treated in the same way as the other phase II samples. Since the surface area sampled at each sampling point was 100 cm^2, seed densities (seeds.m^{-2}) were estimated by multiplying the number of seeds germinating from the samples by 100. For ease of interpretation, at sites where both the 0-5 and 5-10 cm soil layers had been sampled, ie. the Tavistock Woodlands and Werrington Park Estates, the seed bank data for the two layers were combined.

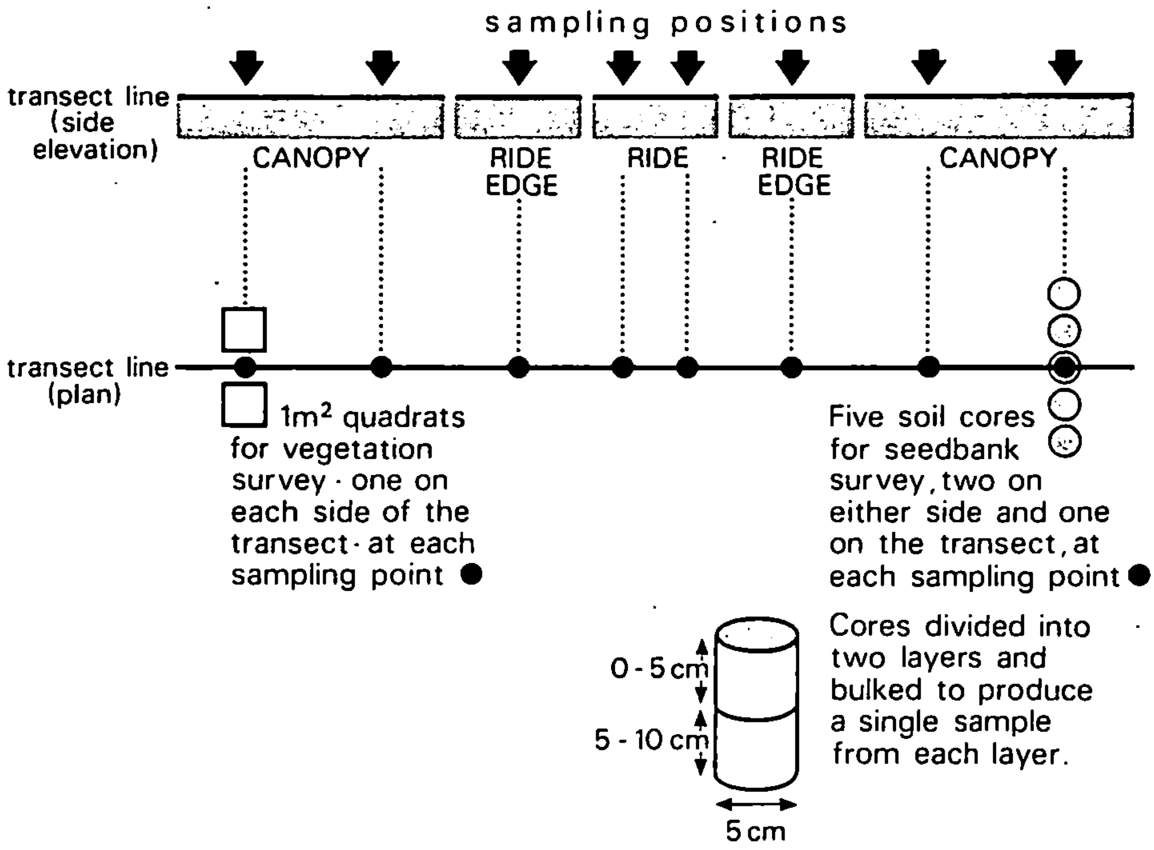


Figure 3.11. Ride survey: Location of quadrats and sampling positions across a ride.

3.5. DATA ANALYSIS

3.5.1. Ground Flora Survey Data

The ground flora data were analysed using TWINSPAN (Two-way Indicator Species Analysis) and DECORANA (Detrended Correspondence Analysis). TWINSPAN is a method of numerical classification which groups quadrats with similar species compositions. DECORANA is a method of ordination which produces a plot of the quadrat groupings. Some of the problems encountered in the application of methods of classification and ordination have been discussed by Gauch (1982), Kershaw & Looney (1985) and Kent & Ballard (1988). Cut levels recommended by Hill (1979b, c) were used: 0, 2, 5, 10 and 20; these are standard levels suitable for percentage cover data. It is necessary to avoid overweighting of the dominant species since British woodlands have a limited number of dominants and as a result there may be a high degree of similarity in the cover species despite differences in ecological conditions.

3.5.2. Seed Bank Survey Data

The seed data from the phase I sampling were also analysed using TWINSPAN and DECORANA, but in this case seed numbers were used instead of percentage cover. The TWINSPAN cut levels were reset to 0, 5, 10, 20 and 50, to cater for the differing distribution of seed bank species abundances.

3.5.3. Comparison of Seed Bank and Ground Flora Survey Data

Rank/abundance plots

Rank/abundance plots for both the ground flora and seed bank data were plotted using combined TWINSPAN abundance scores in order to rank the species.

In a rank/abundance plot the abundance of each species is plotted on a logarithmic scale against the species rank, in order from the most to the least abundant species. This type of species abundance data is generally examined in relation to four models: the log normal distribution, the geometric series, the logarithmic series and MacArthur's broken stick model, as described by Magurran (1988). Each of the four models has a characteristic shape on a rank/abundance plot. The geometric series is represented by a straight line with a steep gradient representing dominance by one or a few species in a species-poor community. The log series and log normal distributions are represented by curves which flatten as the number of species present increases and species of intermediate abundance become more common. The flattest curve is produced by the broken stick model, representing equal species abundances, although in reality species are never uniformly distributed.

Magurran (1981) showed that species abundance of the ground flora in an Irish conifer plantation followed a log series distribution. Most natural communities display a log normal pattern of species abundance, indicating more species and less dominance. For example, the distribution of species abundance of ground flora in an Irish oakwood (Magurran, 1981) was shown to fit a log normal distribution.

The rank/abundance plots were annotated with the species names, as this provided a useful visual aid when comparisons were being made between different sample plots at each site.

<u>Czekanowski similarity coefficients</u>

The diversity, that is the variety and abundance of species, in the seed bank and ground flora was compared using similarity coefficients. The Czekanowski coefficient used by Bray & Curtis (1957) was chosen as a suitable index of diversity. The methods used in the calculation of this coefficient are described by Causton (1988).

One problem with this method is that the ground flora surveys were not intensive enough to record all the species growing at the sites, which tended to make coefficients lower than they really were. Large variations also occur between quadrats because the quadrats are only 1 m^2 and the scale of heterogeneity of the vegetation is different to that of the seed bank. Nevertheless, it was considered important to obtain some numerical measure of the match or overlap between the species and their abundances in the seed bank and ground flora.

3.6. SEED DECAY STUDY

Although the factors responsible for depletion of seeds from the soil are not well understood, a possible cause of seed mortality is attack by seed-decomposing fungi. This was chosen as a topic for investigation.

A series of experiments were carried out to investigate the susceptibility of seeds of a number of woodland ground flora species to attack by a variety of soil fungi. The ground flora species were selected to include some species with short-lived seeds and others with long-lived seeds. Some of the fungi investigated were known to be pathogenic, with the potential to cause seed decay, others to produce antibiotic substances, with the potential to prevent the growth of seed-decomposing fungi. The experimental methods and results of this study are described in chapter seven.

CHAPTER FOUR : SEED BANK AND GROUND FLORA SURVEYS, FIRST YEAR (PHASE I) SAMPLING

4.1. INTRODUCTION

In this chapter the results of the ground flora and seed bank surveys carried out during the phase I sampling are presented. The sampling was carried out at the Werrington Park, Lindridge, Tavistock Woodlands and Longleat Estates. These four sites have been described in section 3.3. At each site, surveys of the seed banks and ground flora under a range of canopy ages and types were carried out. The locations of the sampling plots surveyed at each site are shown in Figures 3.2. to 3.5. The sampling methods used in the surveys have been described in section 3.4. The aim of the phase I sampling was to study the variation within each site in the ground flora and seed banks and to relate this, if possible, to differences in past and present management. More specifically, the purpose was to study differences between even-aged and uneven-aged forestry management systems and to investigate changes in ancient coppices resulting from neglect or conversion to conifers.

4.2. RESULTS

4.2.1. Werrington Park and Lindridge Estates

The data from the seed bank and ground flora surveys from these two sites were analysed in the same way.

Werrington Park Estate

Ground flora survey

In order to define species assemblages and to demonstrate within-site variation, TWo-Way INdicator SPecies ANalysis was applied to the data. The TWINSPAN classification is shown in Table 4.1.; standard cut levels (0, 2, 5, 10, 20) were used. These levels are suitable for woodland ground flora percentage cover data, as explained in section 3.5.1. The eight quadrat groupings can be regrouped into two main groups; A, B, C & D, corresponding to the older spruce and larch canopies and E, F, G & H, corresponding to the young spruce canopies. The first group is characterised by high frequencies and abundances of *Rubus fruticosus* and ferns, particularly *Dryopteris dilatata* and *Pteridium aquilinum*. The sub-groups correspond to the three different sample plots. Group A is distinguished from the others by an abundance of *Oxalis acetosella* and *Hedera helix*. *Oxalis acetosella* is absent from groups B, C & D and *Hedera helix* less abundant or absent. Species which only occur in groups C & D include *Rumex acetosella, Digitalis purpurea* and *Epilobium spp.* The second group is characterised by very low species diversity. The sub-groups (E, F, G & H) are based mainly on differences in the presence and abundance of mosses, stumps and bare soil rather than differences in the ground flora. The two different sample plots cannot be distinguished. The ordination plots (Figures 4.1a. and 4.1b.) show the correspondence between the TWINSPAN groups A, B, C & D and E, F, G & H and the canopy groups for the older spruce and larch plantations and the young spruce plantations respectively. This is an obvious reflection of the difference in the light climate between the young and older canopies.

		quadrats	
		1	
		23334239222222233303338997888889989888997776766679966777766645 4 44456 4455 1115455 1115111455 12	
		6265010823457891390478336312589054406727456901232195417896786226189005747141867183352490246389579350	
1	ATHY FILI	-----3-4--	000000
5	CARE PILU	-----33-------------3---	000000
11	OXAL ACET	42444-4132344243542434--	000000
20	QUER SPP	----3---	000000
10	HEDE HELI	5254444-355-45-354-443-34-32332-4---2---	000001
14	POTE EREC	2-----------------2---------2---	000001
16	AGRO STOL	----------------------------------54--	00001
17	HOLC LANA	----------------------------------43--	00001
28	TEUC SCOR	----------------------4---	00001
3	DRYO DILA	5335554554455555555455---5555445455554555553355555555-----44--	0001
4	PTER AQUI	---45----4-------3-3335555555554555555-4-35554555555555545-3--	0010
26	LONI PERI	32-------------2--------------------------2-----3-3---	0010
6	CYMB MURA	--2---	00110
9	GALI SAXA	------3----------------------------------2----2----------1-2--	00110
7	DIGI PURP	--3---35----44-345443---	00111
8	EPIL SPP	--22-5-------3----1-2---	00111
13	RUME ACET	---3232-------2---33555---	00111
19	LARI SPP	---1--11--	00111
12	RUBU FRUT	555555545554555354454455554555555555555544455553454-35555544421 1---1-----------2222--------1---1---	01
23	MOSS	555555555555545555555555545555555355545555 44555344-44454545-3-332222-------------1-1--434322323422543 3	01
2	DRYO FILI	-------------------------3---2--	100
22	LEAF LITT	554555555555555555545555555555555555555555555555555555555554555555555555555555555555555555555555	100
24	LOGS	--53--44325-3-3234----43445544444-4-----23235445544545344442555555554455553333245554354345333544533	100
15	AGRO CAPI	---2-------------------	101
18	ILEX AQUI	------------------2---1-----1-----1-1---12---2--------------	101
21	BARE SOIL	--2-----3--2----------------2------11222323233	101
27	SOLI VIRG	---2--------1----------------------------	101
25	STUM	44344------------------3------------4454----------------------5533444340--------------------------4	11
		0000000000000000000000000000000000000000000000000000000000001111111111111111111111111111111111111111	
		0000000000000000000000000000000000000000011111111111111111111000000000111111111111111111111111111111	
		0000000000000000000000111111111111111111100000000000000000011100111111100000000000000011111111111111	
		000001111111111111111110000000000000111110000000000000111110111111000000000000001110000000000000011	
		00011000111111111111111000000000001100001000001111111100011 000111000000000011 00000001111111	
		0000000000001110001111111 000110000001 0000001111 01111110000001	
	groups	A B C D E F G H	

Key

% cover	abundance
0	-
1 - 2	1
3 - 5	2
6 - 10	3
11 - 20	4
> 20	5

Table 4.1. TWINSPAN classification of ground flora data from conifer plantations at the Werrington Park Estate.

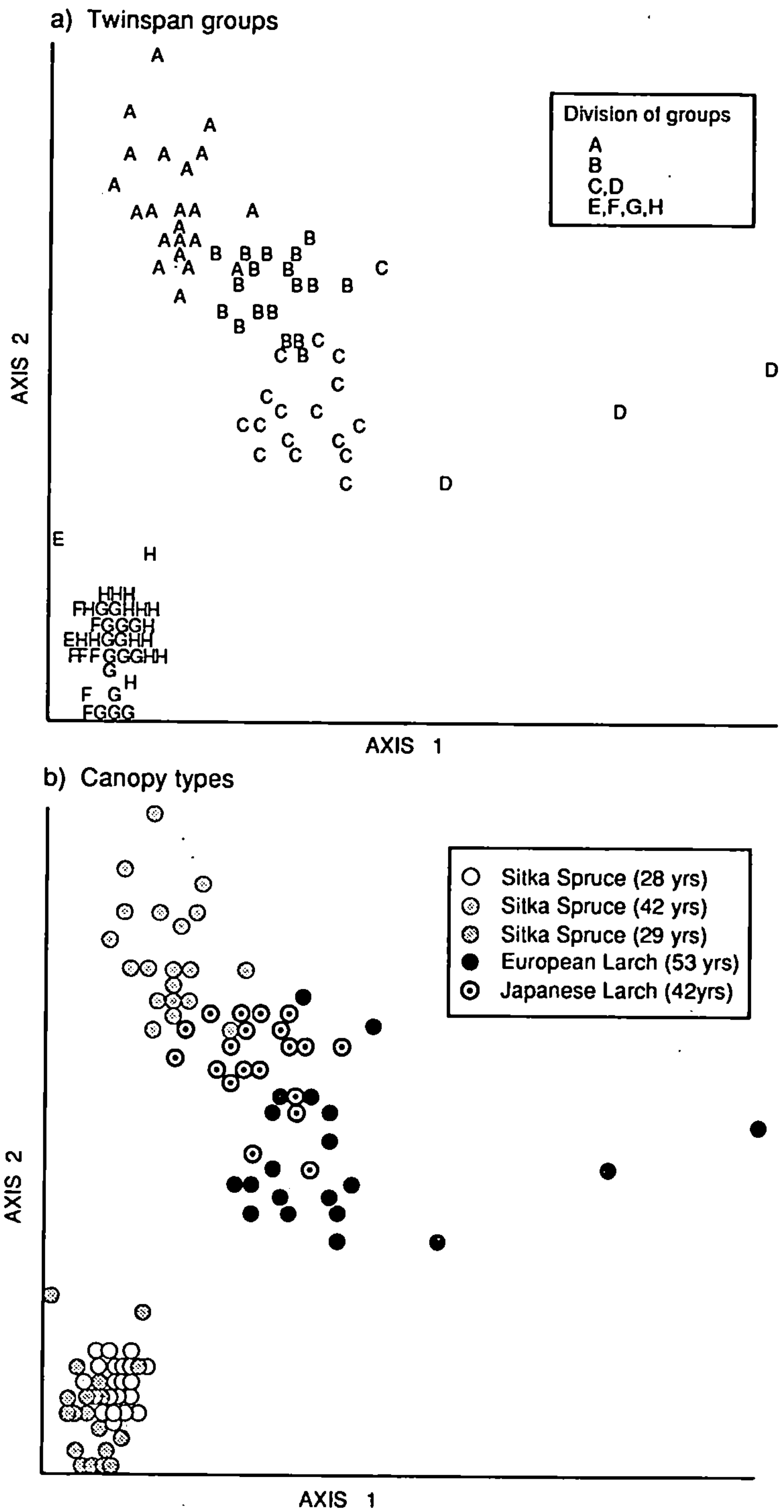


Figure 4.1. DECORANA ordination plots - ground flora survey
Phase I sampling : Werrington Park Estate

Seed bank survey: Soil samples

The TWINSPAN classification is shown in Table 4.2.; non-standard cut levels (0, 2, 5, 20, 50) were used, for the reasons explained in section 3.5.2. The DECORANA ordination plots are shown in Figures 4.2a. and 4.2b. Seed bank groupings show less correspondence to canopy types than ground flora groupings. A number of species, such as *Digitalis purpurea*, *Juncus spp.*, *Rubus fruticosus* and *Agrostis spp.* occur in all, or nearly all, groups. Groups B & C, corresponding to the young spruce canopies, can still be distinguished from groups A, D, E and F, corresponding to the older spruce and larch canopies. The main difference between the young and older plantations is the abundance of *Juncus spp.* (mainly *J. effusus)* in the seed banks of the former. *Calluna vulgaris* and *Galium saxatile* also occur less frequently in groups B & C than in the other groups. Groups A & F, corresponding to the oldest larch plantation, can be distinguished from groups D & E because they are less diverse.

Seed bank survey: Litter samples

The TWINSPAN classification is shown in Table 4.3. and the ordination plots in Figures 4.3a. and 4.3b. Few seeds were present in the litter. As in the soil samples, higher frequencies of *Juncus effusus* in the young spruce plantations (group A in Table 4.3.) distinguish them from the older spruce and larch plantations.

Species present in the ground flora and seed banks

Table 4.4a. shows the species in the ground flora of the two young spruce plantations (Figure 3.3., sampling plots 2 and 4). The ground flora was very sparse beneath the dense canopies at these sites and only seedlings and isolated individuals of shade-tolerant species were present. Table 4.4b. shows the number of seedlings

quadrats

```
                  4454412111111133341333333    12223222222   4  4444
                  45013901347568389021472567834502360145789269812679

17 RUME ACET      443341--------2222----3331---------2----1----231-     111
32 GNAP ULIG      ------------------------1-------------------------    110111
30 LOTU CORN      --------------3--3-3423-2-------------------------    110111
28 SCRO AURI      --------------2------1-21-------------------------    110111
27 CHAM ANGU      -----------------------1--------------------------    110111
26 POLY PERS      --------------------2--1--------------------------    110111
31 STAC SYLV      ----------------32---2----------------------------    110110
29 CIRS ARVE      ---------------1----------------------------------    110110
18 RUME OBTU      ------------1---2---------------------------------    110101
34 LAPS COMM      --------1-----------------------------------------    110100
21 HERA SPHO      -----1--------------------------------------------    110100
20 BETU SPP       ------121221---------111--1-----------------------    110100
 9 LUZU PILO      -----21-------------------------------------------    110100
 4 HOLC LANA      ------------1-11----------------------------------    110100
22 CHEN ALBU      ----2------2--------------------------------------    1100
14 TEUC SCOR      -----11----112-----------1------------------------    1100
12 SILE DIOI      1-------111--23231-1--2---1-1---------1-----------    1100
35 STEL MEDI      -----25-------2-----------------------23----------    101
 8 DIGI PURP      -11--35535334334543443353--22-22-233-33233-21-2---    101
 3 JUNC SPP       1--22555555555555555555555354111331523342333222----   101
 1 RUBU FRUT      -322333322333234-23323233---1--3323333122321--22--    101
 5 POA  ANNU      ---1113132-2---------------------------1--3222-----   100
19 GERA ROBE      ------------1-------------2-----------------------    011
15 ULEX GALL      12-11------1-1------------22-22132-33313-1221--311    011
10 CARE PILU      --------------------2223245-23233435255444223-3----   011
 2 HYPE PULC      ---------------------2---12--3-21-----1----1------    011
 6 AGRO SPP       ---21----1-------23-11-1-1-111133-21-----22332----    010
33 OXAL ACET      -------------------------------1------------------    001
25 POLY AVIC      ------------------------------------1-------------    001
13 CALL VULG      --------12---------------223432555343354233223--1-    001
11 GALI SAXA      ----2---------1----------3441353433-1121433-331-1     001
24 URTI DIOI      -----------------------------------------1--------    000
23 MATR MATR      -----------------------------------------1--------    000
16 POTE EREC      -------------------------------------1---1---1----    000
 7 AGRO CURT      --------------------------1-----------------3-----    000

                  00000000000000000000000000111111111111111111111111
                  00000111111111111111111111000000000000000000001111
                  000110000000001111111111110000000000000000011111
                       00111111110000111111101111111111111110000 1
                           0000111       0000111 011111111111111
                                                 00000000011111

groups             A      B          C             D           E    F
```

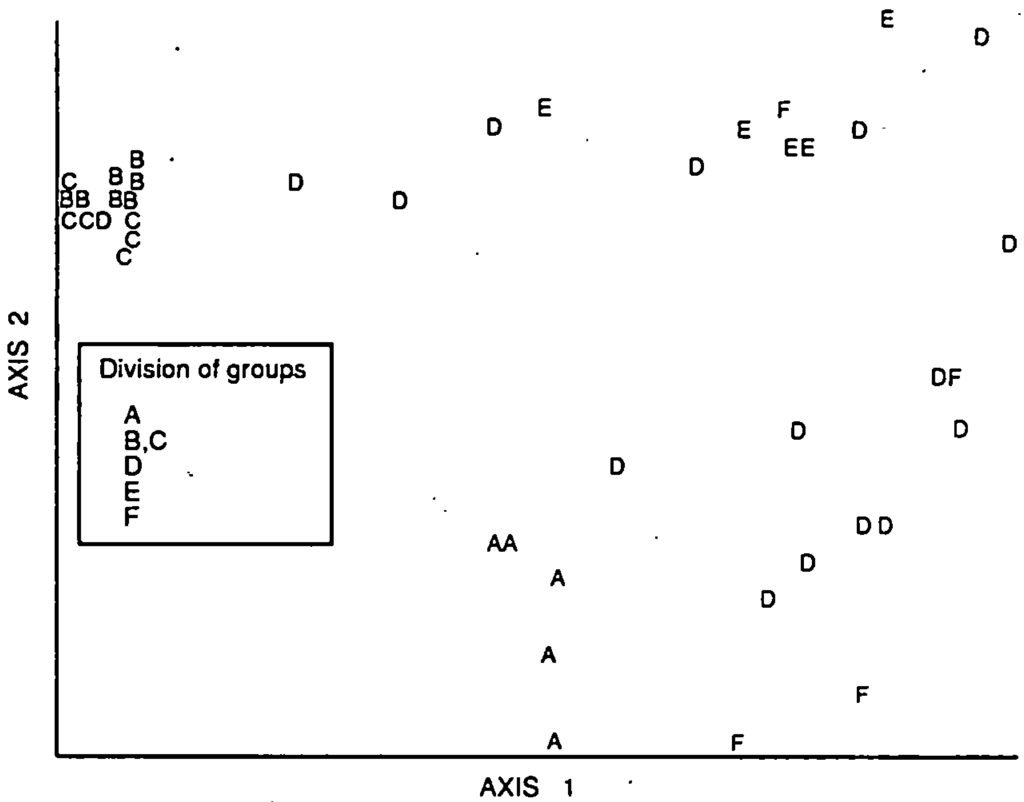
species

Key

% cover	abundance
0	-
1 - 2	1
3 - 5	2
6 - 20	3
21 - 50	4
> 50	5

Table 4.2. TWINSPAN classification of seed bank data (soil samples) from conifer plantations at the Werrington Park Estate.

a) Twinspan groups



b) Canopy types

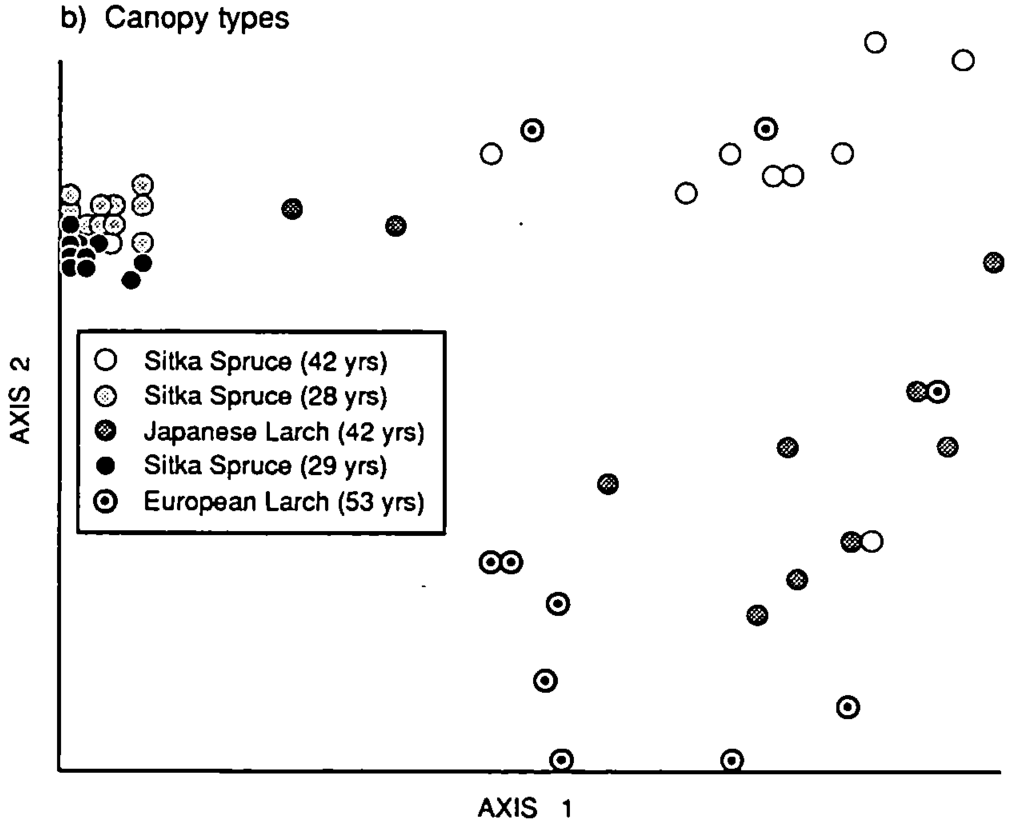


Figure 4.2. DECORANA ordination plots - seed bank survey (soil samples) Phase I sampling : Werrington Park Estate

quadrats

```
                  3333333341223 1|311111221242 |414     124 224445 44|2
                  453812690367732|0567890948625|24094789132145357068|11

11 CHAM ANGU      -11---1------1-|-------------|---------------1----|-   000
 2 JUNC SPP       5355444342111--|-32133--1----|-11-----------------|-   0010
 7 CARE PILU      1------------1-|-------------|--------------------|-   0010
12 RANU REPE      11-------------|-----------1-|--------------------|-   0010
14 SCRO AURI      21-------------|-------------|--------------------|-   0010
 8 SILE DIOI      --1------------|1------------|--------------------|-   0011
22 CYMB MURA      -----11-1------|---------2---|--------------------|-   0011
 5 AGRO CURT      ---------------|-----------1-|--------------------|-   01000
 9 CALL VULG      ---------------|------------1|--------------------|-   01000
17 SENE SYLV      ---------------|----------1--|--------------------|-   010010
19 RUME OBTU      ---------------|--------1----|--------------------|-   010010
15 PLAN MAJO      ---------------|----1--------|--------------------|-   010011
20 CIRS ARVE      ---------------|--2----------|--------------------|-   010011
21 CHEN ALBU      ---------------|---1---------|--------------------|-   010011
23 STEL MEDI      ---------------|14453453-----|--------------------|-   010011
10 BETU SPP       ---------------|--2-2-1-1-1--|1-------------------|-   0101
 6 DIGI PURP      ----1-1------11|-1-----1111-1|31------------------|-   011
18 OXAL ACET      ---------------|------------2|--------------1-----|-   011
 3 POA  ANNU      ---------------|-1-3123-2431-|-----------331233111|-   10
 1 RUBU FRUT      1---1--------1-|-2-21--------|211111122332321221--|-   11
 4 AGRO SPP       --1-----------1|-------------|----------3--------1|-   11
13 HYPO RADI      ---------------|-------------|------------1-------|1   11
16 RUME ACET      ---------------|-------------|-------------1---2--|1-  11

                  000000000000000|0000000000000|11111111111111111111|1
                  000000000000000|1111111111111|00000000000000000000|1
                  000000000000001|1000000000000|10000000000000000001|
                  0011111111111  |000000000001 |00000001111111111111|
                    00000001111  |0000000111   |00111110000111111111|
                    0011111      |01111111     |  00111     00000011|

groups                  A        |      B      |         C          |D
```

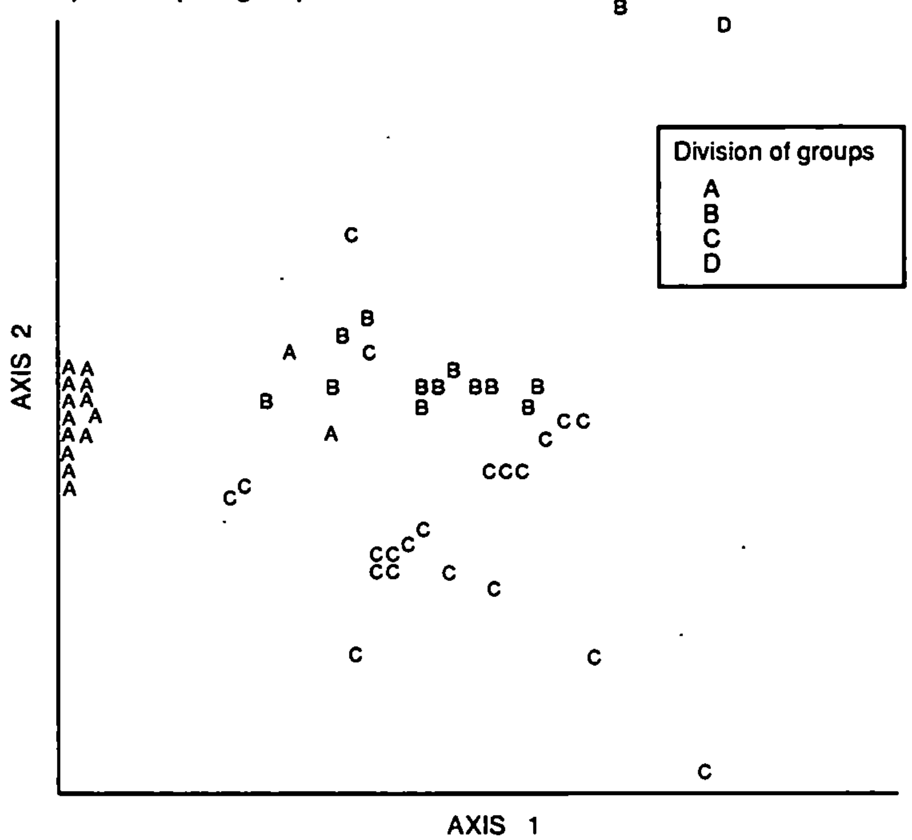
species

Key

% cover	abundance
0	-
1 - 2	1
3 - 5	2
6 - 20	3
21 - 50	4
> 50	5

Table 4.3. TWINSPAN classification of seed bank data (litter samples) from conifer plantations at the Werrington Park Estate.

b) Twinspan groups



a) Canopy types

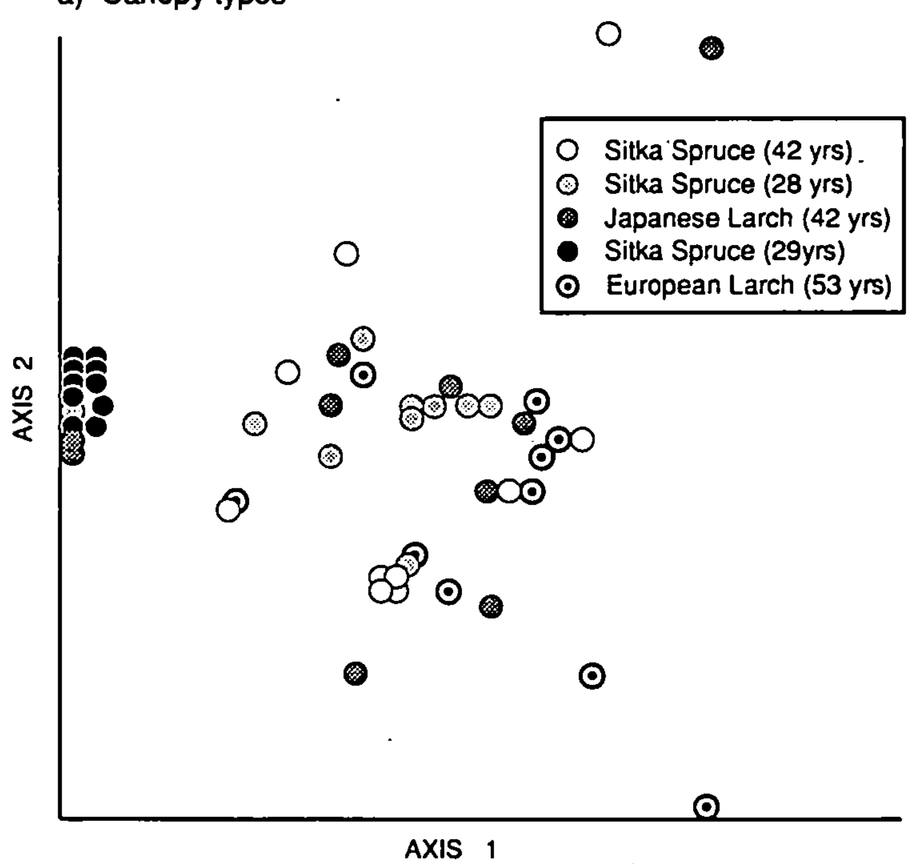


Figure 4.3. DECORANA ordination plots - seed bank survey (litter samples)
Phase I sampling : Werrington Park Estate

Table 4.4a. Species in the ground flora in the young conifer plantations at the Werrington Park Estate.

Species	Sitka spruce 28 yrs	Sitka spruce 29 yrs
Agrostis capillaris	-	+
Dryopteris filix-mas	+	-
Ilex aquifolium	+	+
Rubus fruticosus	+	+
Solidago virgaurea	-	+
Total no. of species	3	4

Table 4.4b. Numbers of seedlings in germination tests in the young conifer plantations at the Werrington Park Estate (Phase I sampling).

Species	Sitka spruce 28 yrs		Sitka spruce 29 yrs	
	i	ii	i	ii
Agrostis spp.	6	1	7	1
Betula spp.	9	6	5	-
Calluna vulgaris	3	-	-	-
Carex pilulifera	2	-	145	1
Chamaenerion angustifolium	-	-	1	3
Chenopodium album	3	1	-	-
Cirsium arvense	-	2	1	-
Cymbalaria muralis	-	-	-	3
Digitalis purpurea	356	3	249	2
Galium saxatile	1	-	1	-
Geranium robertianum	1	-	-	-
Gnaphalium uliginosum	-	-	1	-
Heracleum sphondylium	1	-	-	-
Holcus lanatus	2	-	1	-
Hypericum pulchrum	-	-	4	-
Juncus effusus/bufonius	2719	33	7697	368
Lapsana communis	1	-	-	-
Luzula pilosa	3	-	-	-
Lotus corniculatus	-	-	85	-
Plantago major	-	1	-	-
Poa annua	26	34	-	-
Polygonum persicaria	-	-	3	-
Ranunculus repens	-	-	-	2
Rubus fruticosus	76	7	105	2
Rumex obtusifolius	2	1	-	-
Rumex acetosella	-	-	36	-
Scrophularia auriculata	-	-	7	3
Silene dioica	16	-	26	1
Stachys sylvatica	-	-	14	-
Stellaria media	64	280	2	-
Teucrium scorodonia	6	-	-	-
Ulex gallii	2	-	-	-
Total no. of seeds	3299	369	8390	394
Seeds.m^{-2}	32990	3690	83900	3940
Total no. of species	20	11	19	12

i Soil samples (0-5 cm)
ii Litter samples

recorded in the germination tests from the soil and litter samples. Table 4.5a. shows the species in the ground flora for the older spruce plantation and the two larch plantations (Figure 3.3. sampling plots 1, 3 and 5). Under these more open canopies the ground flora was more abundant and diverse. Table 4.5b. shows the number of seedlings recorded in the germination tests from the soil and litter samples.

The sparse ground floras of the young spruce plantations were effectively indistinguishable. For the older spruce and larch canopies, differences in the ground floras of the three sample plots were slight. The most abundant species were *Rubus fruticosus*, *Dryopteris dilatata*, *Pteridium aquilinum* and *Hedera* helix. The oldest larch canopy was the most open and several species characteristic of woodland clearings were present, such as *Digitalis purpurea*, *Rumex acetosella* and *Epilobium spp*.

The seed banks of the young spruce plantations were dominated by *Juncus effusus* and *Digitalis purpurea*. *Carex pilulifera* and *Rubus fruticosus* were also abundant. Different abundances of *Juncus effusus* account for most of the variation in seed numbers between the two sample plots. In the older spruce and larch plantations the most abundant species in the seed banks were *Juncus effusus*, *Calluna vulgaris*, *Carex pilulifera* and *Galium saxatile*. The number of seeds and species present under the oldest larch canopy was significantly lower than under the two younger canopies. Despite the open conditions which exist, it appears that the seed bank has become depleted beneath this canopy, while remaining relatively undepleted in the younger plantations. Two species, *Calluna vulgaris* and *Ulex gallii*, were well represented in the seed banks but absent from the ground flora. Other species common in the seed

Table 4.5a. Species in the ground flora in the older conifer plantations at the Werrington Park Estate.

Species	Sitka spruce 42 yrs	Japanese larch 42 yrs	European larch 53 yrs
Agrostis capillaris	-	-	+
Agrostis stolonifera	-	+	-
Athyrium filix-femina	+	+	-
Carex pilulifera	+	-	-
Cymbalaria muralis	-	-	+
Digitalis purpurea	-	-	+
Dryopteris dilatata	+	+	+
Dryopteris filix-mas	-	+	-
Epilobium spp.	-	-	+
Galium saxatile	+	-	+
Hedera helix	+	+	+
Holcus lanatus	-	+	+
Hyacinthoides non-scripta	+	+	+
Ilex aquifolium	+	-	+
Lonicera periclymenum	+	+	+
Oxalis acetosella	+	+	-
Potentilla erecta	+	+	-
Pteridium aquilinum	+	+	+
Rubus fruticosus	+	+	+
Rumex acetosella	-	-	+
Teucrium scorodonia	-	+	-
Total no. of species	12	13	14

Table 4.5b. Numbers of seedlings in germination tests in the older conifer plantations at the Werrington Park Estate (Phase I sampling).

Species	Sitka spruce 42 yrs		Japanese larch 42 yrs		European larch 53 yrs	
	i	ii	i	ii	i	ii
Agrostis spp.	25	-	18	10	8	1
Betula spp.	-	1	-	-	-	1
Calluna vulgaris	84	1	490	-	3	-
Carex pilulifera	63	1	388	-	-	-
Chamaenerion angustifolium	-	1	-	-	-	1
Chenopodium album	-	-	-	-	2	-
Cymbalaria muralis	-	-	-	3	-	-
Digitalis purpurea	26	18	53	2	6	2
Galium saxatile	158	-	125	-	17	-
Geranium robertianum	3	-	-	-	-	-
Hypericum pulchrum	25	-	2	-	-	-
Hypochoeris radicata	-	-	-	2	-	-
Juncus effusus/bufonius	344	1	137	2	10	1
Larix spp.	-	-	-	2	-	1
Matricaria matricarioides	1	-	-	-	-	-
Oxalis acetosella	1	2	-	-	-	1
Poa annua	12	8	1	31	5	47
Polygonum aviculare	-	-	1	-	-	-
Potentilla erecta	2	-	1	-	-	-
Ranunculus repens	-	-	-	1	-	-
Rubus fruticosus	9	15	59	16	30	13
Rumex acetosella	-	-	-	-	122	3
Rumex obtusifolius	1	-	4	1	-	-
Silene dioica	2	-	1	1	1	-
Senecio sylvaticus	-	-	-	-	-	1
Stellaria media	-	-	13	11	-	-
Teucrium scorodonia	1	-	-	-	-	-
Ulex gallii	15	-	43	-	18	-
Urtica dioica	1	-	-	-	-	-
Total no. of seeds	773	48	1336	82	222	72
Seeds.m^{-2}	7730	480	13360	820	2220	720
Total no. of species	18	9	15	12	11	11

i Soil samples (0-5cm)
ii Litter samples

banks such as *Juncus effusus*, *Silene dioica* and *Digitalis purpurea* were either absent or poorly represented in the ground flora beneath the canopies, but abundant in nearby rides and clearings.

Rank/abundance plots

Rank/abundance plots, based on TWINSPAN abundance scores, for the ground flora and soil seed bank in the five sample plots are shown in Figures 4.4a. and 4.4b. The low numbers of seeds in the litter precluded this type of data presentation.

The interpretation of these rank/abundance plots was explained in section 3.5.3. Most of the plots fit the log series model. The exceptions are the seed bank of the oldest larch plantation, and the ground flora of the two young spruce plantations, which conform to the species-poor geometric series.

Czekanowski similarity coefficients

Czekanowski similarity coefficients were calculated using combined TWINSPAN abundance scores to indicate the degree of similarity in species composition and abundance of the ground flora and seed bank for each of the sample plots. The results are shown in Table 4.6. The use of these coefficients was discussed in section 3.5.3. Values near to 0 indicate little similarity.

The coefficients are generally low, due in the youngest plantations to the sparsity of the ground flora and in the older plantations to differences in the species which dominate the ground flora and the seed banks. In the ground flora, the ferns *Dryopteris dilatata* and *Pteridium aquilinum*, and *Rubus fruticosus*, are abundant. In

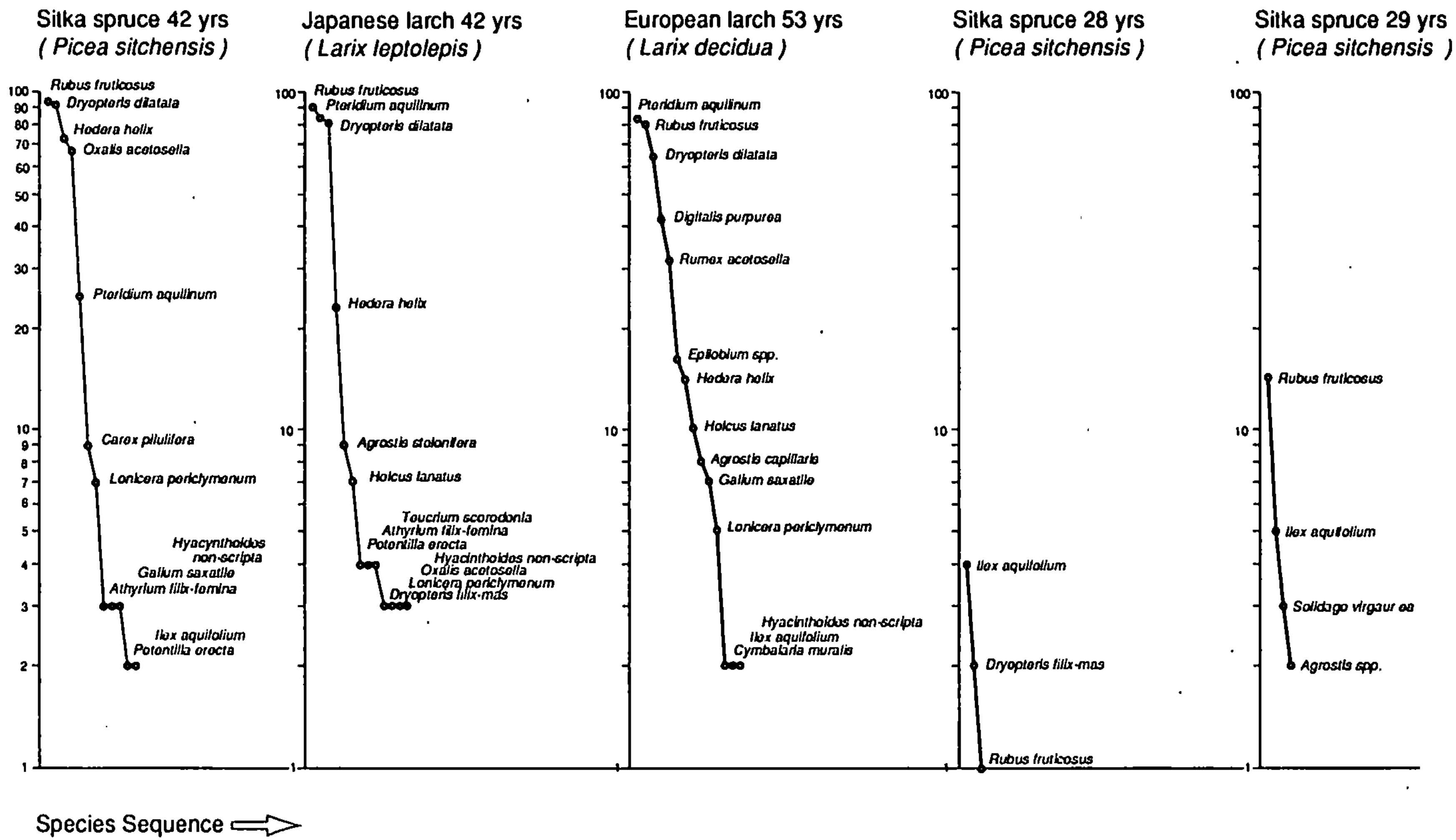


Figure 4.4a. Rank/abundance plot. Werrington Park Estate. Ground flora species.

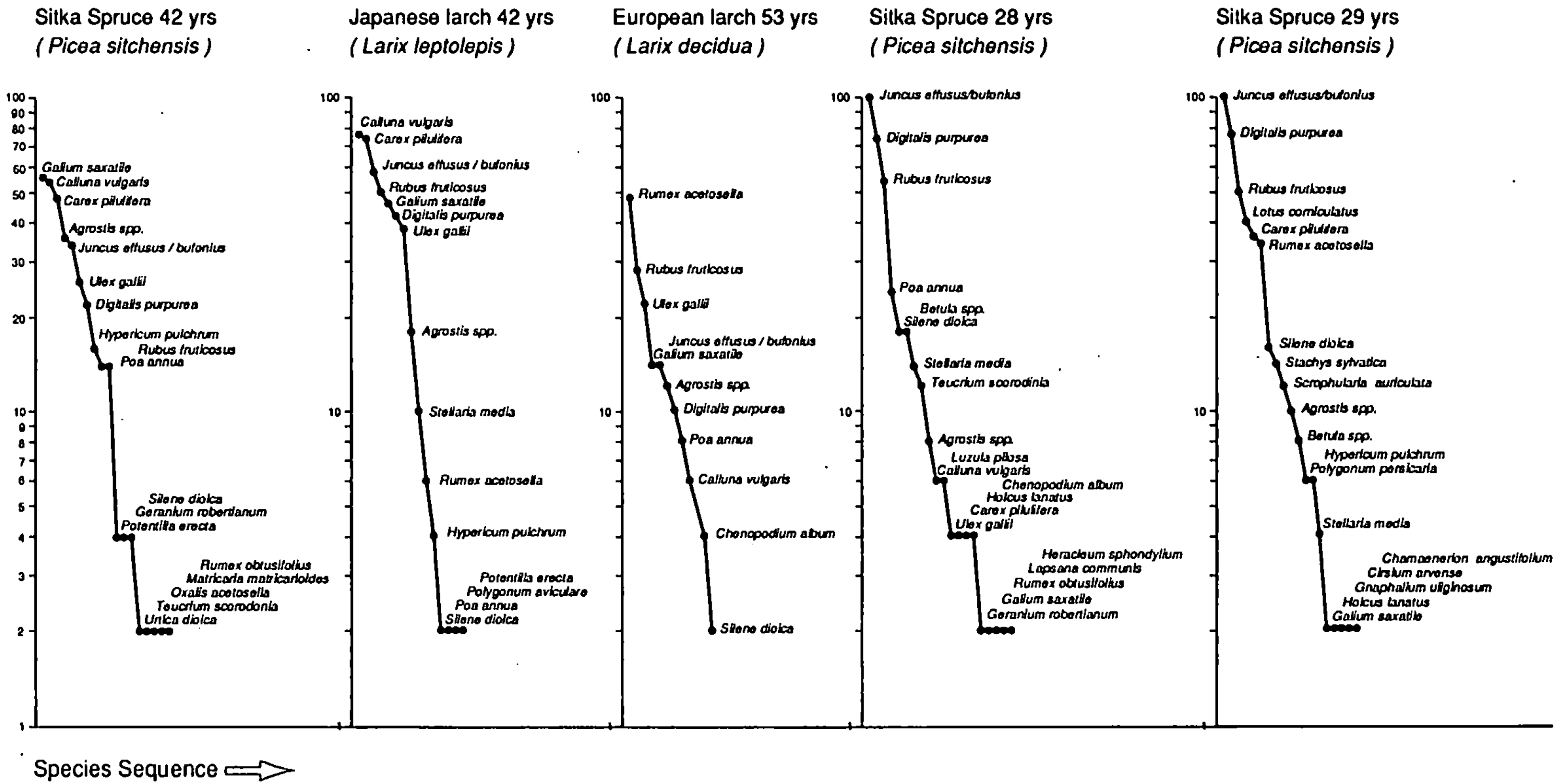


Figure 4.4b. Rank/abundance plot. Werrington Park Estate. Seed bank species.

Table 4.6. Czekanowski similarity coefficients indicating the degree of similarity in species composition and abundance between the ground flora and soil seed bank for the Werrington Park Estate (Phase I sampling).

Canopy Type	Age	Coefficient (C)
Sitka spruce	28 yrs	0.0054
Sitka spruce	29 yrs	0.0711
Sitka spruce	42 yrs	0.0833
Japanese larch	42 yrs	0.1622
European larch	53 yrs	0.3017

$C = 2W/A+B$

Where
A = the sum of species scores in the ground flora.
B = the sum of species scores in the seed bank.
W = the sum of the lesser score of those species which occur in both.

the seed banks, the dominant species include *Calluna vulgaris*, *Juncus effusus*, *Carex pilulifera* and *Galium saxatile*, all of which are absent from or poorly represented in the ground flora. The coefficient for the oldest plantation is slightly higher due to the high abundance of *Rumex acetosella* and *Rubus fruticosus* in both the seed bank and the ground flora.

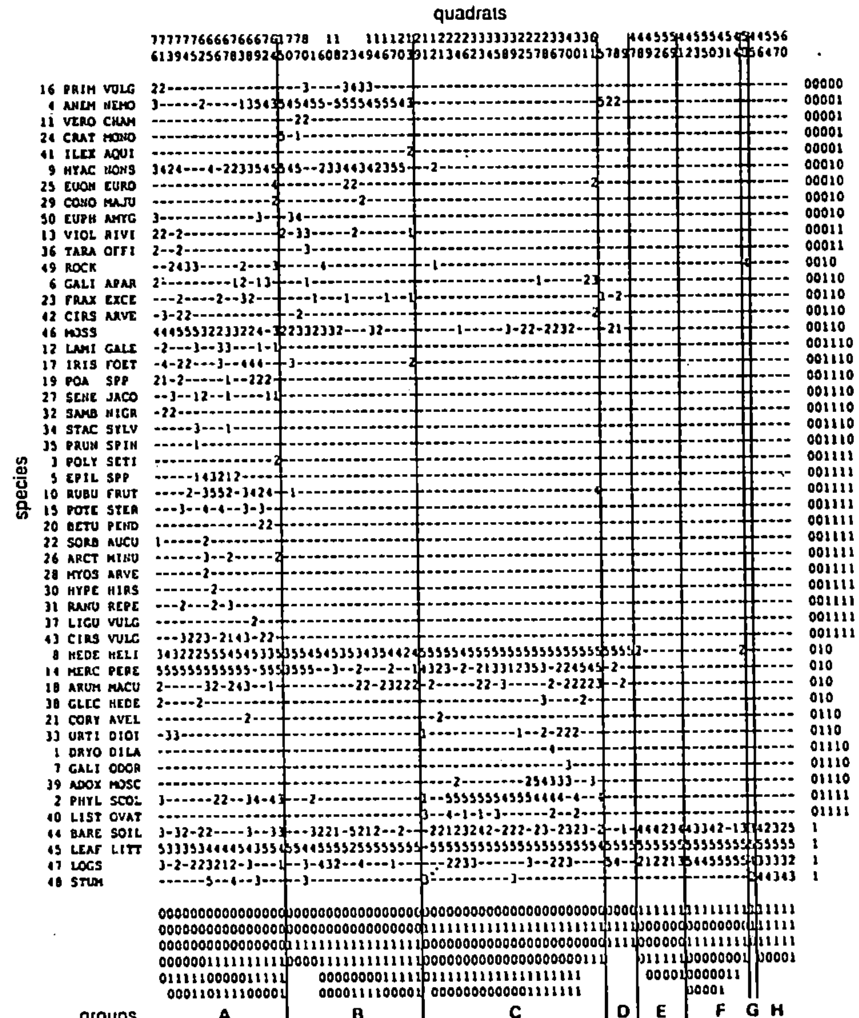
Lindridge Estate

Ground flora survey

The TWINSPAN classification is shown in Table 4.7., cut levels used were: 0, 2, 5, 10, 20. The eight quadrat groupings show a clear gradient of ground flora species diversity. From group A, which corresponds to the felled area, diversity declines progressively through group B and groups C & D; these groups correspond to the abandoned coppice and the larch plantation respectively. Groups E, F, G & H, which are virtually devoid of ground flora, correspond to the Douglas fir plantation. The ordination plots (Figures 4.5a. and 4.5b.) show the correspondence between the four TWINSPAN groups and the four canopy types.

Seed bank survey: Soil samples

The TWINSPAN classification is shown in Table 4.8., cut levels used were: 0, 2, 5, 20, 50. The ordination plots are shown in Figures 4.6a. and 4.6b. The only group that corresponds well to a canopy type is group A (abandoned coppice) which has a lower species diversity than the other groups. Group B is much more diverse and groups C & D intermediate. There are no other obvious differences between the seed



Key

% cover	abundance
0	.
1 - 2	1
3 - 5	2
6 - 10	3
11 - 20	4
> 20	5

Table 4.7. TWINSPAN classification of ground flora data from conifer plantations, abandoned coppice and felled area at Buckley Wood on the Lindridge Estate.

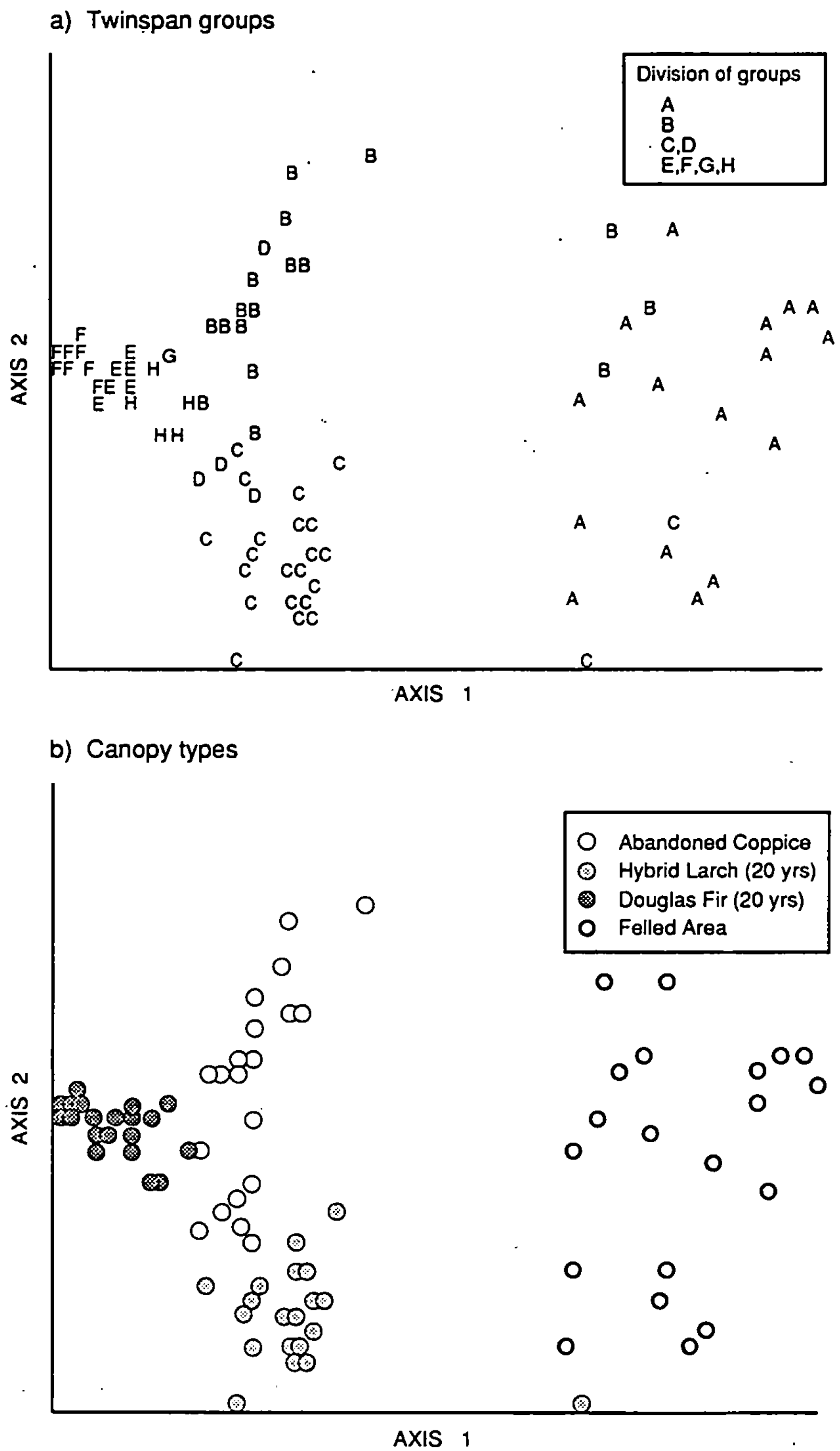


Figure 4.5. DECORANA ordination plots - ground flora survey
Phase I sampling : Lindridge Estate

```
                                     quadrats
                  33222222223111311211 2 11  1 3       33433
                  83342561890345769712087859074234611126059

 1 RUBU FRUT      1--22341-2--111-21111222232214532 2---21-    000
33 BETU PEND      -245434433322222-23123233-331122--2222222    0010
 7 RANU REPE      1---1--1---------------------1------------   00110
18 PRIM VULG      -------1-11-----------1------1------------   00110
20 HYPO RADI      -------1----------------------------------   00110
10 ANAG ARVE      ------------------------------2-----------   00111
34 BUDD DAVI      -----1-1----11-11------1-1----------------   00111
 2 HYPE PERF      -------21222213-23232434535452441411-2----   0100
31 RUME ACET      --------1--2---222333232-------212---12--    0100
35 MOEH TRIN      -----------11---------------2-------1-----   0100
17 SILE DIOI      ---------------11-1-1-------------------1-   0101
32 SAMB NIGR      ---------------211-----2------------------   0101
 8 EUPA CANN      -----------1--------1--------2----11------   011
22 URTI DIOI      -----------51341------2311---12---1-2142     011
 3 SCRO NODO      -----------------------------1------1-------  10000
 6 HOLC LANA      -------------------------------1-------1------  10000
39 GEUM URBA      -----------1-----------------------1----------  10000
40 STEL MEDI      -----------------------------122--2-2-1-------  10000
30 CARE FLAC      --------------------------------11-21---------  10001
 4 POA  SPP       --11----11-------------11-----433322------2   1001
23 CHAM ANGU      2--------------1-----------------12----------1  1001
25 EUPH AMYG      ----------1-----------1--11--12222------1-    1001
12 CIRS ARVE      --12---------1-----1---1112-11-332-222-1-    101
24 IRIS FOET      -1----------------1-------------------1-1----  1100
14 AJUG REPT      -------------1----------------------------1---  11010
11 POTE STER      -----------------------1--------------1-1----  11011
16 CLEM VITA      ----------------1-------------------------1-1-  11011
19 SENE SYLV      ----------------1-------------------------2----  11011
37 CENT ERYT      -----------2------------------------1---1-2-  11011
 5 AGRO STOL      ----------------------------1-----1-----4    111000
13 CIRS VULG      ----------------------------13-122333222     111001
15 CARD HIRS      ------------------------------------------1---  111001
27 VERO PERS      ------------------------------------------1---  111001
36 SENE JACO      -----------------------------------------23-1--  111001
21 CHEN ALBU      ----------------------------1-----------1---  11101
28 VERO CHAM      -------------------1----------1--2----21--   11101
 9 ARCT MINU      -------------------------------2211------     1111
26 VERO OFFI      ------------------------------1---2------    1111
29 VERO MONT      -------------------------1---212---------    1111
38 VIOL RIVI      ----------------------------------1------    1111

                  00000000000000000000000000000111111111111
                  00000000000111111111111111110000000111111
                  01111111111000000000011111110000010000111
                   000000111100001111110000000101111
                   011111         01111100011
                    00111           00111
        groups         A              B            C     D
```

Key

% cover	abundance
0	-
1 - 2	1
3 - 5	2
6 - 20	3
21 - 50	4
> 50	5

Table 4.8. TWINSPAN classification of seed bank data (soil samples) from conifer plantations, abandoned coppice and felled area at Buckley Wood on the Lindridge Estate.

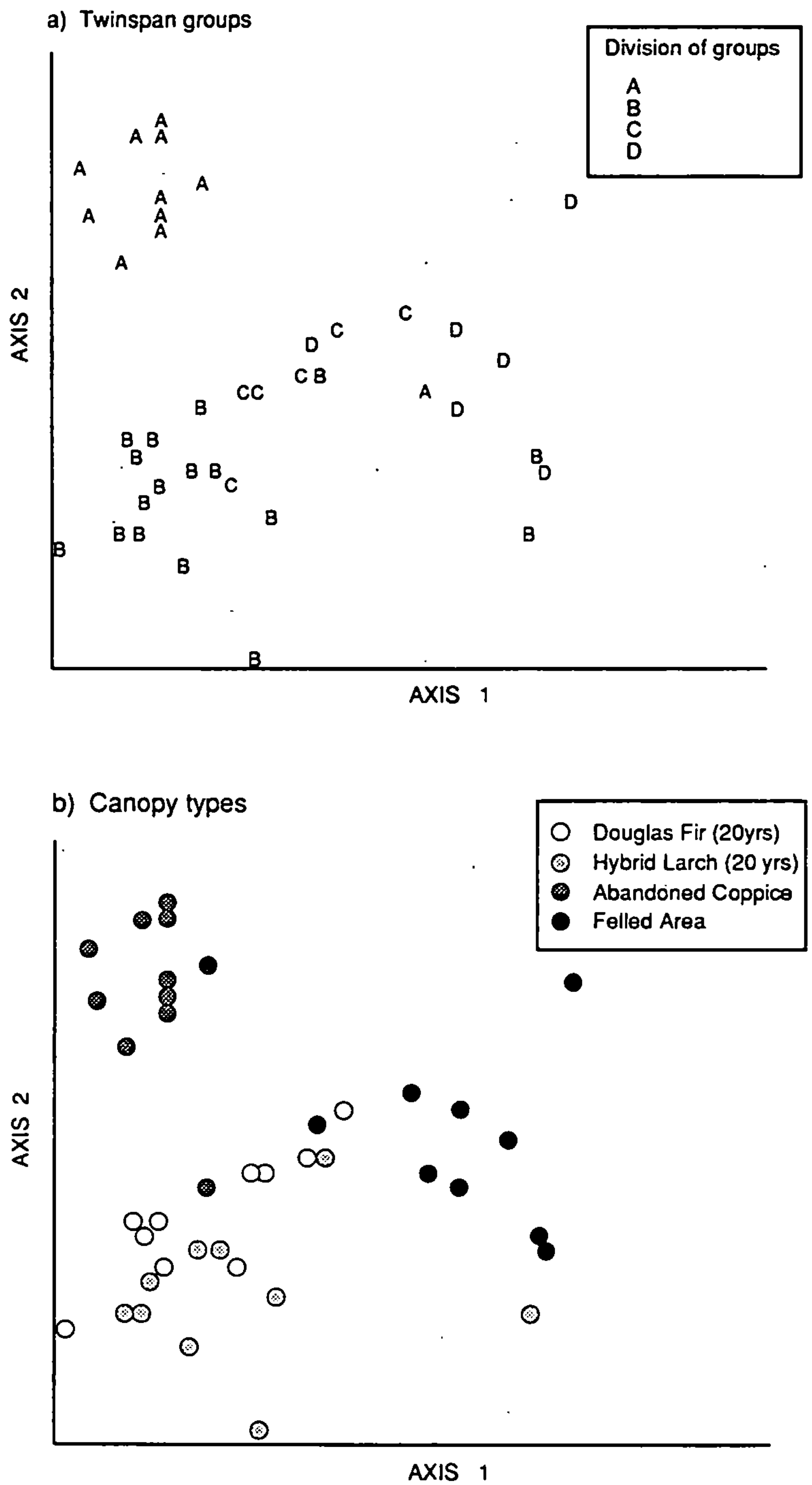


Figure 4.6. DECORANA ordination plots - seed bank survey (soil samples)
Phase I sampling : Lindridge Estate

banks of the different canopy types. Common species occurring in all groups include *Rubus fruticosus*, *Betula pendula*, *Rumex acetosa* and *Hypericum perforatum*.

Seed bank survey: Litter samples

The TWINSPAN classification is shown in Table 4.9. Seed numbers in the litter samples were low. The main division (group B in Table 4.9) is due to the presence of *Betula* seeds. The ordination plots (Figures 4.7a. and 4.7b.) show that there is no correspondence between the TWINSPAN groups and the canopy types.

Species in the ground flora and seed banks

Table 4.10a. shows the species in the ground flora of the conifer plantations (Figure 3.5., sampling plots 3 and 4). Table 4.10b. shows the number of seedlings recorded in the germination tests from the soil and litter samples. Table 4.11a. shows the species in the ground flora of the felled area and the abandoned coppice (Figure 3.5., sampling plots 1 and 2). Table 4.11b. shows the number of seedlings recorded in the germination tests from the soil and litter samples.

The ground floras beneath the four different canopy types were distinct. The Douglas fir plantation was virtually devoid of ground flora because of the dense shade. The only species present was *Hedera helix*. In the larch plantation and the abandoned coppice, a limited ground flora of mainly shade-tolerant species was present, including *Hedera helix*, *Mercurialis perennis* and *Arum maculatum*. *Anemone nemorosa* and *Hyacinthoides non-scripta* were also very common in the abandoned coppice and *Adoxa moschatellina* and *Listera ovata* in the larch plantation. In contrast, the ground

quadrats

```
                  33332222        12 112222233311111133 1134
                  31291578469123704557023690786813456829 40

 3 POA  SPP       ----------------------------------------31  1
 1 RUBU FRUT      --------13-------------------------------1  01
15 FRAX EXCE      -----111--------1-------------------------  00111
 8 SENE JACO      -12----1----------------------------------  00111
 5 AJUG REPT      ----1--1----------------------------------  00111
13 BETU PEND      -1-1111-33222112211111111111111-1---------  00110
12 SAMB NIGR      ------------------------------12----------  00110
 4 CIRS ARVE      --------121-------------------------------  0010
 2 HYPE PERF      ----------1-12211------------------1------  0010
14 BUDD DAVI      ----------1---------------------------1---  00011
10 URTI DIOI      ------------------------------1-111-------  00011
 7 CLEM VITA      ---------1-1---1-------------------1--111--  00011
 6 CARD HIRS      ------------------------------------111-1---  00011
11 CHAM ANGU      -111------2-------------------11-11-------  00010
 9 MYOS ARVE      2-------------1---------------------------  0000

                  00000000000000000000000000000000000000011
                  01111111111111111111111111111111111111
                   00000000000000000000000000000001111111
                   00000001111111111111111111111110000111
                   000111100000000000011111111111100111
                       00011111110000000000011

         groups  A|               B              |   C  |D
```

% cover	abundance
0	-
1 - 2	1
3 - 5	2
6 - 20	3
21 - 50	4
> 50	5

Key

Table 4.9. TWINSPAN classification of seed bank data (litter samples) from conifer plantations; abandoned coppice and felled area at Buckley Wood on the Lindridge Estate.

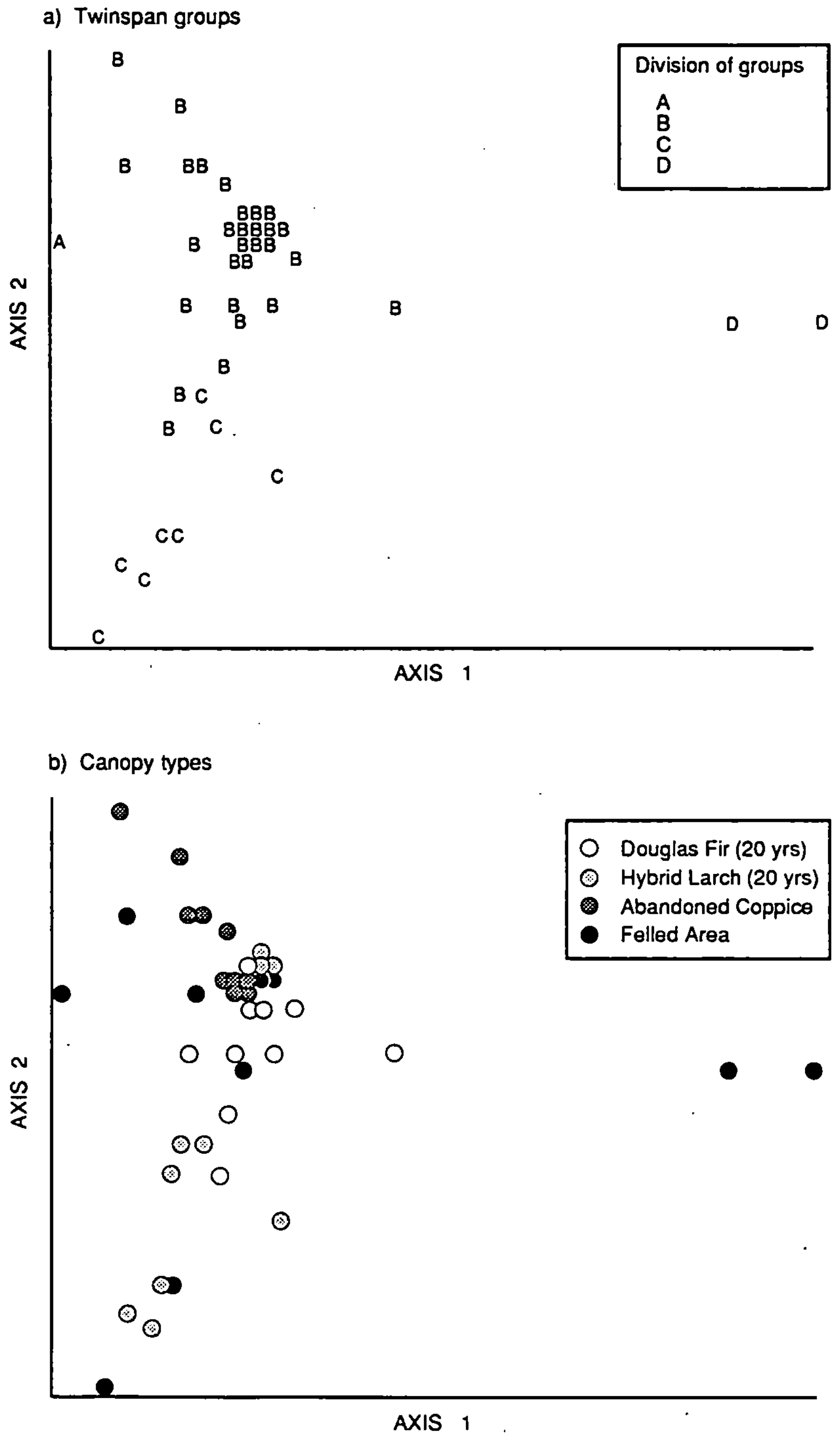


Figure 4.7. DECORANA ordination plots - seed bank survey (litter samples) Phase I sampling : Lindridge Estate

Table 4.10a. Species in the ground flora in conifer plantations at Buckley Wood on the Lindridge Estate.

Species	Douglas fir	Hybrid larch
Adoxa moschatellina	-	+
Arum maculatum	-	+
Dryopteris dilatata	-	+
Galium aparine	-	+
Galium odoratum	-	+
Glechoma hederacea	-	+
Hedera helix	+	+
Listera ovata	-	+
Mercurialis perennis	-	+
Phyllitis scolopendrium	-	+
Urtica dioica	-	+
Total no. of species	1	11

Table 4.10b. Numbers of seedlings in germination tests in conifer plantations at Buckley Wood on the Lindridge Estate (Phase I sampling).

Species	Douglas fir		Hybrid larch	
	i	ii	i	ii
Agrostis stolonifera	1	-	-	-
Anagallis arvensis	2	-	-	-
Arctium minus	6	-	-	-
Betula pendula	27	33	32	6
Buddleja davidii	1	1	5	1
Carex flacca	5	-	-	-
Cardamine hirsuta	-	-	-	2
Centaurium erythraea	1	-	2	-
Chamaenerion angustifolium	2	3	1	2
Cirsium arvense	20	6	4	-
Cirsium vulgare	14	-	-	-
Clematis vitalba	-	4	-	3
Eupatorium cannabinum	4	-	2	-
Euphorbia amygdaloides	2	-	-	-
Geum urbanum	1	-	1	-
Holcus lanatus	2	-	-	-
Hypericum perforatum	133	10	99	-
Iris foetidissima	1	-	1	-
Moehringia trinervia	3	-	2	-
Myosotis arvensis	-	1	-	-
Poa annua/trivialis	26	-	1	-
Potentilla sterilis	2	-	-	-
Primula vulgaris	2	-	-	-
Psuedotsuga menziesii	-	1	-	-
Ranunculus repens	1	-	-	-
Rubus fruticosus	80	7	13	-
Rumex acetosa	11	-	37	-
Sambucus nigra	-	-	7	3
Scrophularia nodosa	-	-	-	-
Silene alba	-	-	4	-
Stellaria media	12	2	-	-
Urtica dioica	6	-	46	4
Veronica chamaedrys	4	-	1	-
Veronica officinalis	3	-	-	-
Veronica montana	6	-	-	-
Viola riviniana	1	-	-	-
Total no. of seeds	391	68	258	21
Seeds.m^{-2}	3910	680	2580	210
Total no. of species	30	10	17	7

i Soil samples (0-5cm)
ii Litter samples

Table 4.11a. Species in the ground flora in the felled area and abandoned coppice at Buckley Wood on the Lindridge Estate.

Species	Felled area	Abandoned coppice
Anemone nemorosa	+	+
Ajuga reptans	+	-
Arctium minus	+	-
Arum maculatum	+	+
Betula pendula	+	-
Cirsium arvense	+	-
Cirsium vulgare	+	-
Conopodium majus	+	+
Corylus avellana	+	+
Crataegus monogyna	+	+
Fraxinus excelsior	+	+
Epilobium spp.	+	-
Euonymus europaeus	+	+
Euphorbia amygdaloides	+	-
Galium aparine	+	-
Glechoma hederacea	+	-
Hedera helix	+	+
Hyacinthoides non-scripta	+	+
Hypericum hirsutum	+	-
Hypericum montanum	+	-
Hypericum perforatum	+	-
Ilex aquifolium	-	+
Iris foetidissima	+	+
Ligustrum vulgare	+	-
Lamiastrum galeobdolon	+	-
Mercurialis perennis	+	+
Myosotis arvensis	+	-
Phyllitis scolopendrium	+	-
Poa annua	+	-
Poa trivialis	+	-
Polystichum setiferum	+	-
Potentilla sterilis	+	-
Primula vulgaris	+	+
Prunus spinosa	+	-
Ranunculus repens	+	-
Ranunculus ficaria	+	+
Rosa canina	+	-
Rubus fruticosus	+	-
Ruscus aculeatus	+	-
Sambucus nigra	+	-
Senecio jacobaea	+	-
Solanum dulcamara	+	-
Sorbus aucuparia	+	-
Stachys sylvatica	+	-
Taraxacum officinale	+	-
Urtica dioica	+	-
Veronica chamaedrys	+	-
Veronica montana	+	-
Veronica officinalis	+	-
Veronica persica	+	-
Viola riviniana	+	+
Total no. of species	51	15

Table 4.11b. Numbers of seedlings in germination tests in the felled area and abandoned coppice at Buckley Wood on the Lindridge Estate (Phase I sampling).

Species	Felled area		Abandoned coppice	
	i	ii	i	ii
Agrostis stolonifera	13	-	-	-
Ajuga reptans	2	-	-	2
Betula pendula	22	4	28	10
Buddleja davidii	-	-	2	-
Cardamine hirsuta	1	2	-	-
Centaurium erythraea	3	-	-	-
Chamaenerion angustifolium	6	4	-	-
Chenopodium album	2	-	-	-
Cirsium arvense	9	-	3	-
Cirsium vulgare	2	-	-	-
Clematis vitalba	2	-	1	-
Euphorbia amygdaloides	2	-	1	-
Fraxinus excelsior	-	-	-	5
Hypericum perforatum	4	-	10	-
Hypochoeris radicata	-	-	1	-
Iris foetidissima	2	-	-	-
Moehringia trinervia	1	-	-	-
Myosotis arvensis	-	2	-	-
Poa annua/trivialis	1	9	4	-
Potentilla sterilis	1	-	-	-
Primula vulgaris	-	-	3	-
Ranunculus repens	1	-	2	-
Rubus fruticosus	8	1	30	-
Rumex acetosa	3	-	3	-
Sambucus nigra	-	-	1	-
Senecio jacobaea	14	4	-	1
Senecio sylvaticus	2	-	1	-
Silene alba	1	-	-	-
Urtica dioica	36	-	-	-
Veronica chamaedrys	3	-	-	-
Veronica persica	1	-	-	-
Total no. of seeds	178	26	190	18
Seeds.m^{-2}	1780	260	1900	180
Total no. of species	25	7	14	4

i Soil samples (0-5cm)
ii Litter samples

flora of the felled area was more diverse and both light-demanding and shade-tolerant species were present.

Differences in the seed banks were less clear-cut. The plantations have apparently not reached a sufficient age to affect the seed banks adversely. The seed bank beneath the Douglas fir plantation was as diverse as that of the felled area. Fewer species were recorded in the seed bank of the larch plantation. The 'missing' species were generally those which were present in the Douglas fir plantation in low numbers, so this lack of diversity could be attributable to the patchiness of the seed bank and the chance recording of species in the Douglas fir plantation but not in the larch plantation. As shown in Figure 3.5., the Douglas fir plantation and the felled area were adjacent to fields, whereas the abandoned coppice and larch plantation were not; it is in these former areas that weed seeds, such as *Anagallis arvensis*, *Chenopodium album* and *Stellaria media* were present in the soil. The seed bank of the abandoned coppice was significantly less diverse than the seed banks of the other canopy types, indicating that seed bank depletion has occurred in this part of the wood.

<u>Rank/abundance plots</u>

Rank/abundance plots for the ground flora and soil seed bank in the abandoned coppice, recently felled area and the larch plantation are shown in Figures 4.8a. and 4.8b. The lack of ground flora in the Douglas fir plantation rendered it unsuitable for this method of data presentation, although the soil seed bank data were plotted. The low numbers of seeds in the litter in all four sample plots precluded this type of data presentation.

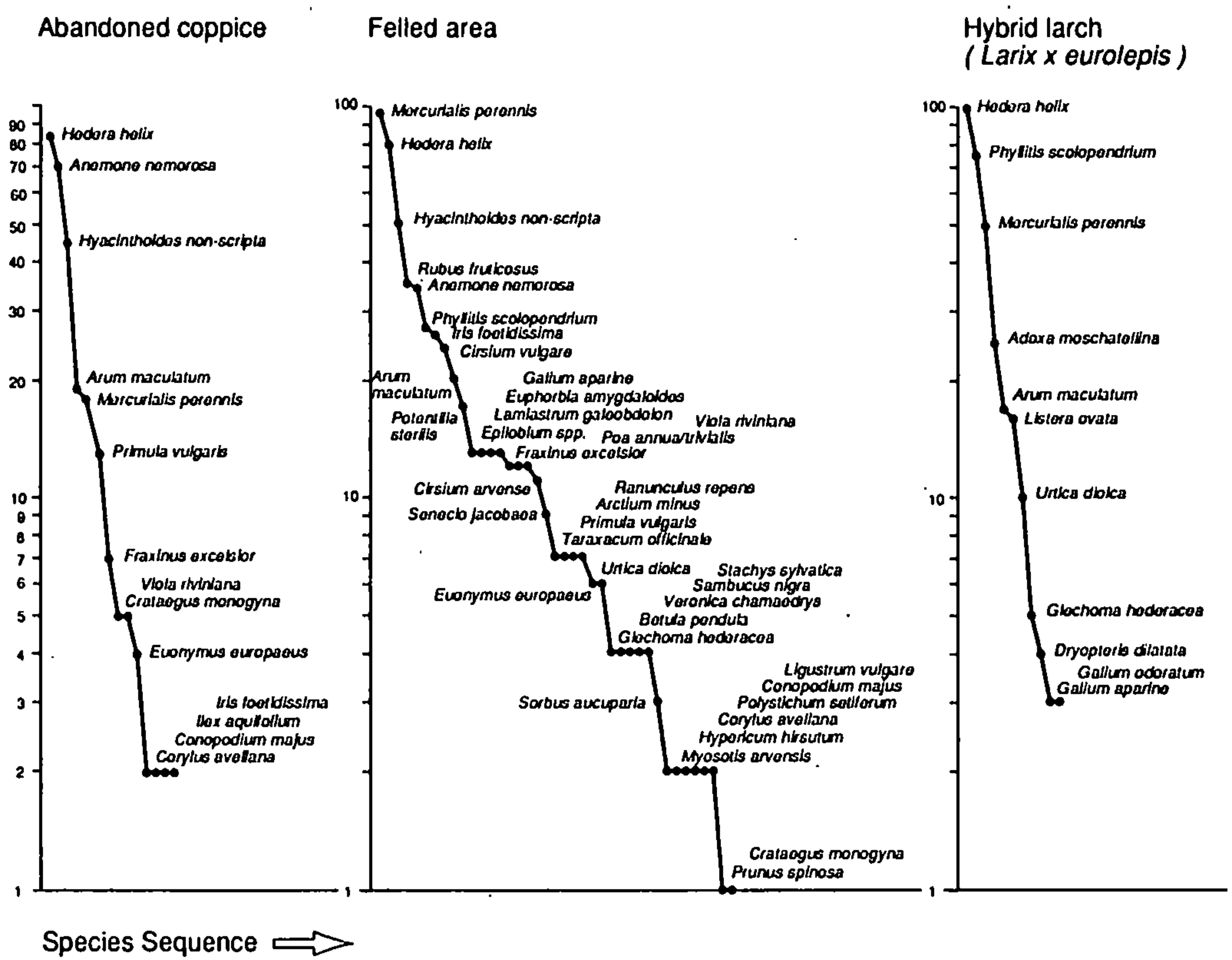


Figure 4.8a. Rank/abundance plot : Lindridge Estate. Ground flora species

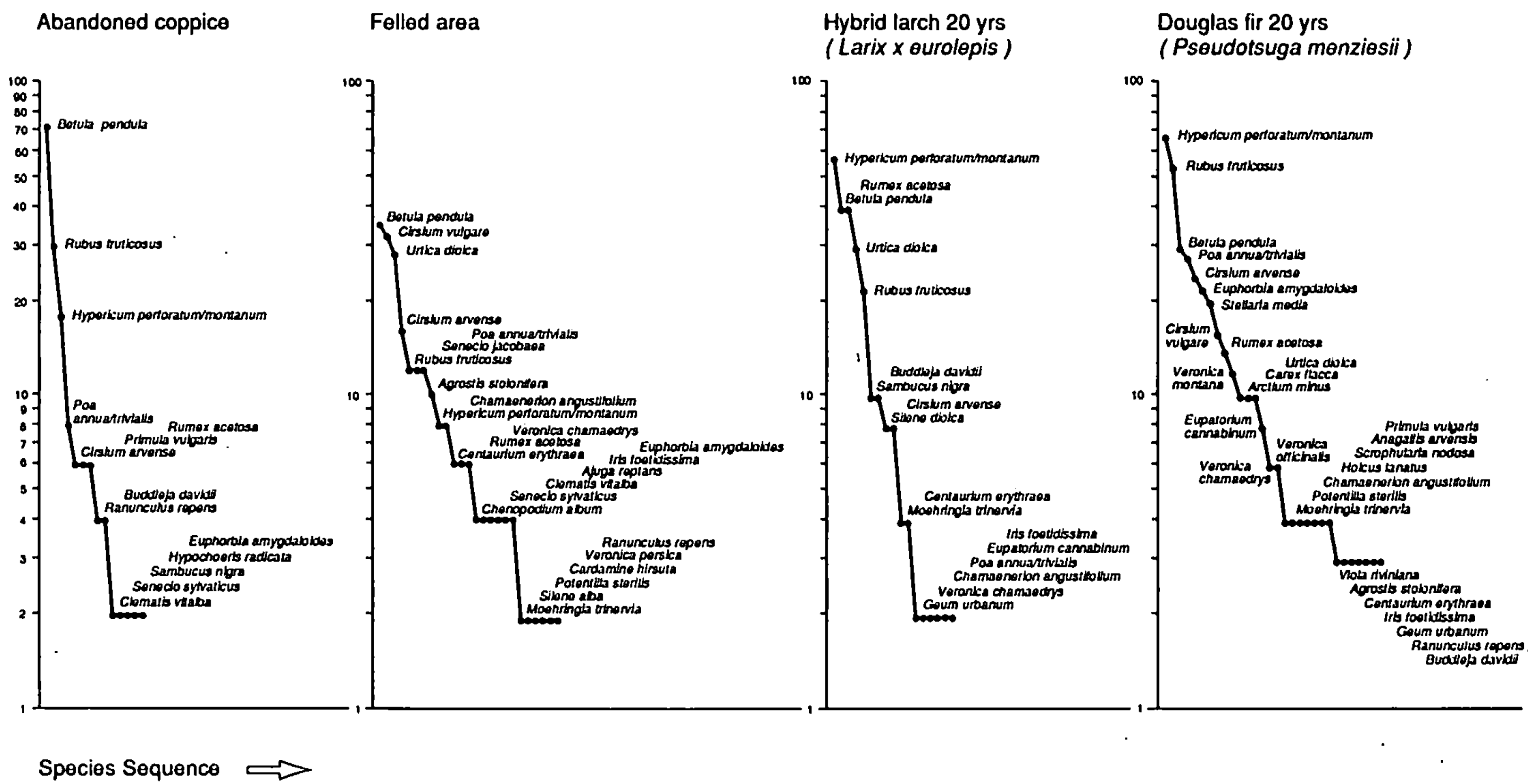


Figure 4.8b. Rank/abundance plot : Lindridge Estate. Seed bank species

The rank/abundance plots for the seed banks all fit the log series model. The plot for the ground flora of the larch plantation fits the geometric model and that for the abandoned coppice the log series model. The plot for the more diverse ground flora of the felled area conforms to the log normal distribution. For the felled area, the number of ground flora species listed in Table 4.11a. is actually much higher than the number shown in the rank/abundance plot. This is because the rank/abundance plots are based on TWINSPAN abundance scores. At this site, the ground flora survey was carried out in the early spring. Additional species present in the floristically rich felled area were observed on subsequent visits to the site.

Czekanowski similarity coefficients

Czekanowski similarity coefficients are shown in Table 4.12. The coefficients for the conifer plantations and the abandoned coppice are low, due to the sparsity of the ground flora in the Douglas fir plantation and, in the abandoned coppice and larch plantation, to the dominance of shade-tolerant and vernal ground flora species such as *Hedera helix*, *Anemone nemorosa*, *Mercurialis perennis* and *Hyacinthoides non-scripta*, which are not represented in the seed bank. The slightly higher coefficient for the felled area indicates the greater overlap of species composition between the more diverse ground flora and the seed bank, although the most abundant species in the ground flora are still *Hedera helix*, *Mercurialis perennis* and *Hyacinthoides non-scripta*.

Table 4.12. Czekanowski similarity coefficients indicating the degree of similarity in species composition and abundance between the ground flora and soil seed bank for the Lindridge Estate (Phase I sampling).

Canopy type	Age	Coefficient (C)
Douglas fir	20 yrs	0.0000
Hybrid larch	20 yrs	0.0361
Abandoned coppice		0.0271
Felled area		0.2231

$$C = 2W/A+B$$

Where
A = the sum of species scores in the ground flora.
B = the sum of species scores in the seed bank.
W = the sum of the lesser score of those species which occur in both.

4.2.2. Tavistock Woodlands and Longleat Estate

Since low numbers of seeds germinated from the phase I samples from these two sites, the data were unsuitable for analysis using TWINSPAN and DECORANA. The phase II sampling, the results of which are presented in chapter five, provided an opportunity to assess whether the poor germination resulted from the inferior environment of the shade tunnel used for the phase I samples from these two sites or whether there were simply few seeds in the soil.

Tavistock Woodlands Estate

Table 4.13a. shows the species in the ground flora of the B-Plan sub-units (I to V). The data for the four units have been combined. There is a clear trend from low species diversity in the older, darker sub-units to higher diversity in the younger, more open sub-units, in which a number of species become more abundant, for example *Calluna vulgaris*, *Carex pilulifera*, *Digitalis purpurea*, *Hypericum pulchrum*, *Juncus effusus* and *Teucrium scorodonia*. These species, characteristic of oak coppice, are all light-demanding species which have small seeds and are represented in the seed bank. Table 4.13b. shows the number of seedlings recorded in the germination tests from the soil and litter samples. As in the pilot study, for most species there were no differences in the seed banks in the different sub-units, with the exceptions of *Juncus effusus* and *Agrostis spp.* (*A. capillaris* and *A. stolonifera*) which were more abundant in seed bank of the younger sub-units. The trend for higher numbers of seeds of *Agrostis spp.* in the younger, more open sub-units has already been demonstrated in the pilot study (chapter two).

Table 4.13a. Species in the ground flora of four Bradford Plan units at Blanchdown and Grenoven Woods on the Tavistock Woodlands Estate. I-V represent B-Plan stages.

Species	I 27 yrs	II 21 yrs	III 15 yrs	IV 9 yrs	V 3 yrs
Agrostis capillaris	-	+	+	-	+
Agrostis stolonifera	-	+	+	+	+
Athyrium filix-femina	-	-	+	-	-
Betula pendula/pubescens	-	-	+	+	+
Blechnum spicant	+	+	+	+	+
Calluna vulgaris	-	+	-	+	+
Carex pilulifera	+	-	+	-	+
Deschampsia flexuosa	-	+	+	-	-
Digitalis purpurea	-	-	-	-	+
Dryopteris dilatata	+	+	+	+	+
Dryopteris filix-mas	-	+	+	+	+
Epilobium spp.	-	-	+	-	-
Hedera helix	+	+	+	+	+
Hypericum pulchrum	-	-	-	+	+
Ilex aquifolium	-	+	-	-	+
Juncus effusus	-	-	-	-	+
Lonicera periclymenum	+	+	+	+	+
Luzula pilosa	+	+	+	+	+
Melampyrum pratense	-	-	+	+	+
Oxalis acetosella	-	-	-	-	+
Potentilla erecta	-	-	+	-	-
Pteridium aquilinum	+	+	+	+	+
Quercus spp.	-	-	+	+	+
Rubus fruticosus	+	+	+	+	+
Solidago virgaurea	-	-	+	+	+
Sorbus aucuparia	-	-	+	+	-
Teucrium scorodonia	-	-	-	+	+
Vaccinium myrtillus	+	+	+	+	+
Total no. of species	9	14	21	18	23

Table 4.13b. Number of seedlings in germination tests in four Bradford Plan Units at Blanchdown and Grenoven Woods on the Tavistock Woodlands Estate (Phase I sampling). I-V represent B-Plan stages.

i Soil samples

Species	I 27 yrs	II 21 yrs	III 15 yrs	IV 9 yrs	V 3 yrs
Agrostis spp.	8	11	9	88	73
Betula spp.	-	1	-	-	-
Calluna vulgaris	4	8	-	2	1
Carex pilulifera	15	10	26	6	3
Digitalis purpurea	1	3	10	9	35
Hypericum pulchrum	6	4	2	7	34
Juncus effusus	37	8	30	214	162
Luzula pilosa	17	4	15	7	8
Rubus fruticosus	36	21	21	74	41
Teucrium scorodonia	-	-	-	-	1
Ulex gallii	1	2	1	3	-
Total no. of seeds	125	72	114	410	358
Seeds.m^{-2}	1563	900	1425	5125	4475
Total no. of species	9	10	8	9	9

ii Litter samples

Species	I 27 yrs	II 21 yrs	III 15 yrs	IV 9 yrs	V 3 yrs
Agrostis spp.	2	2	1	4	-
Betula spp.	-	1	1	1	1
Digitalis purpurea	3	2	-	-	4
Geranium robertianum	-	2	-	-	-
Juncus effusus	1	-	9	-	2
Luzula pilosa	-	2	1	-	2
Rubus fruticosus	-	4	-	2	8
Total no. of seeds	6	13	12	7	17
Seeds.m^{-2}	75	163	150	88	213
Total no. of species	3	6	4	3	5

Table 4.14a. shows the species in the ground flora of abandoned coppice and recently cut coppice (Figure 3.2., sampling plots 2 and 3). The rank/abundance plot is shown in Figure 4.9. The ground flora survey was carried out in the second year following cutting but no marked increase in species diversity had taken place on the cut plot. *Rubus fruticosus* had become the dominant species in the ground flora and most of the other species present were shade-tolerant species such as *Hedera helix*, *Lonicera periclymenum* and *Vaccinium myrtillus*. Of these, only *Rubus fruticosus* was also present in the seed bank. The ability of this species to retain viable seeds in the soil, combined with a capacity to spread vegetatively, explains its success in dominating the ground flora of cleared woodland. *Agrostis capillaris*, a species characteristic of open conditions, had also become more abundant in the ground flora of the cut plot. The shade-intolerant *Calluna vulgaris* was not abundant on the cut plot; *Calluna vulgaris* would probably have been more abundant in the ground flora when the coppice was worked, but declined beneath the dark canopy of the abandoned coppice. It is likely that there had been insufficient time for recolonisation of this species to occur on the cut plot. The presence of an appreciable amount of *Calluna vulgaris* in the abandoned coppice plot indicates that the canopy was not very dark in the sampled area.

Table 4.14b. shows the number of seedlings recorded in the germination tests from the soil and litter samples. It appears that the seed bank had become depleted at this site as a result of the long period of neglect. *Calluna vulgaris* was the only species which was abundant in the seed bank in either of the sample plots. It has been shown, for example by Darby (1987) and Granstrom (1988), that the seeds of this species can remain viable for long periods of time in the soil. Higher densities of *Calluna* seeds

Table 4.14a. Species in the ground flora in cut and abandoned coppice at Blanchdown Wood on the Tavistock Woodlands Estate.

Species	Cut coppice	Abandoned coppice
Agrostis capillaris	+	-
Betula pendula/pubescens	+	-
Calluna vulgaris	+	+
Castanea sativa	-	+
Corylus avellana	+	-
Dryopteris filix-mas	-	+
Fagus sylvatica	+	+
Hedera helix	+	+
Ilex aquifolium	+	+
Lonicera periclymenum	+	-
Melampyrum pratense	+	+
Pteridium aquilinum	-	+
Quercus spp.	+	+
Rubus fruticosus	+	+
Sorbus aucuparia	-	+
Vaccinium myrtillus	+	+
Total no. of species	12	12

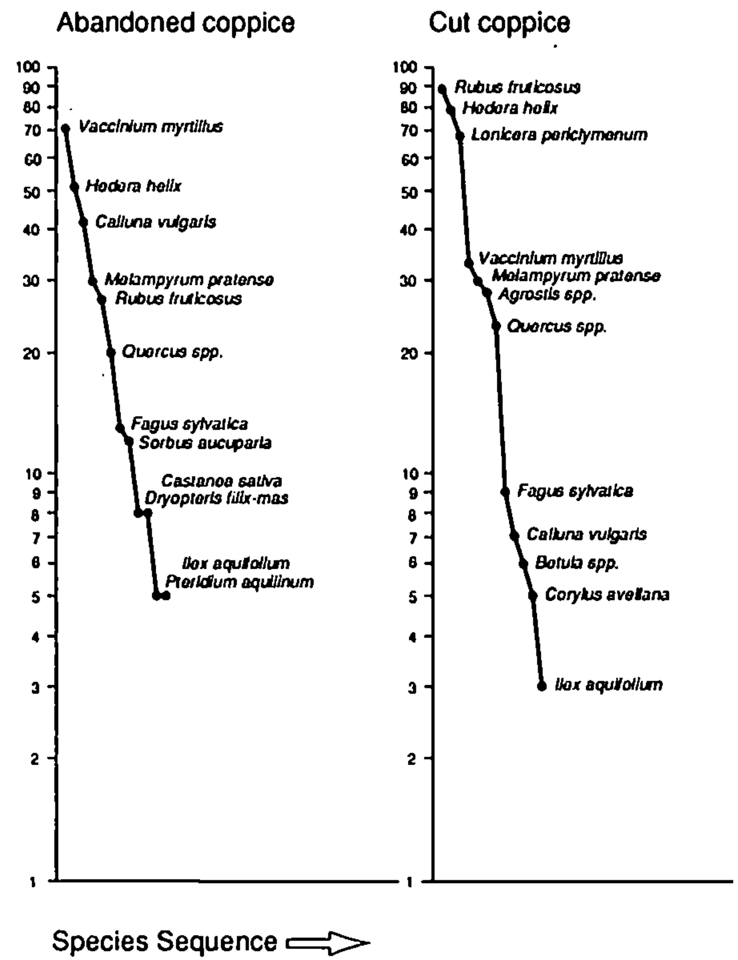


Figure 4.9. Rank/abundance plot. Tavistock Woodlands Estate. Ground flora species.

Table 4.14b. Number of seedlings in germination tests in cut and abandoned coppice at Blanchdown Wood on the Tavistock Woodlands Estate (Phase I sampling).

Species	Cut coppice		Abandoned coppice	
	i	ii	i	ii
Agrostis capillaris	2	-	-	-
Betula spp.	2	2	-	2
Calluna vulgaris	44	-	24	-
Rubus fruticosus	1	-	6	-
Total no. of seeds	49	2	247	2
Seeds.m^{-2}	490	20	2470	20
Total no. of species	4	1	2	1

i Soil samples (0-5 cm)
ii Litter samples

were recorded in the uncut plot, where the species was much more abundant in the ground flora.

Longleat Estate

Table 4.15a. shows the species in the ground flora of the even-aged and uneven-aged conifers (Figure 3.4., sampling plots 3 and 4). The rank/abundance plot is shown in Figure 4.10a. Under the dark canopy of the even-aged Douglas fir plantation the ground flora was patchy and species-poor; shade-tolerant *Blechnum spicant*, *Rhododendron ponticum* and *Rubus fruticosus* were present. Under the open canopy of the uneven-aged conifers the ground flora was much more diverse. Grasses, particularly *Agrostis capillaris*, *A. stolonifera* and *Deschampsia flexuosa*, were abundant and *Calluna vulgaris* was also common. Table 4.15b. shows the number of seedlings recorded in the germination tests from the soil and litter samples. There were fewer species represented in the seed bank of the even-aged conifer plantation than in the uneven-aged stand. However, this may be due to the poor germination from the samples; since the species absent from the even-aged plantation were only present in low numbers in the uneven-aged stand.

Table 4.16a. shows the species in the ground flora of the oak stands (Figure 3.4., sampling plots 1 and 2). The rank/abundance plot is shown in Figure 4.10b. One sample plot is in a stand which had been thinned and pruned, making the canopy more open. The other is in stand which had not been managed recently. Although many species in the ground flora are common to both stands, the ground flora of the managed stand is more diverse and includes a number of shrub and understorey species which are absent from the unmanaged stand.

Table 4.15a. Species in the ground flora in even-aged and uneven-aged conifers on the Longleat Estate.

Species	Even-aged conifers	Uneven-aged conifers
Acer pseudoplatanus	-	+
Agrostis capillaris	-	+
Agrostis stolonifera	-	+
Betula pendula/pubescens	-	+
Blechnum spicant	+	-
Calluna vulgaris	-	+
Carex demissa	-	+
Carex pilulifera	+	+
Carpinus betulus	-	+
Deschampsia flexuosa	-	+
Digitalis purpurea	-	+
Dryopteris affinis	-	+
Dryopteris dilatata	-	+
Dryopteris filix-mas	-	+
Fagus sylvatica	-	+
Galium saxatile	-	+
Glechoma hederacea	-	+
Hedera helix	+	-
Holcus lanatus	-	+
Holcus mollis	-	+
Hypericum pulchrum	-	+
Ilex aquifolium	-	+
Lonicera periclymenum	-	+
Oxalis acetosella	-	+
Potentilla erecta	-	+
Pteridium aquilinum	-	+
Quercus spp.	-	+
Rhododendron ponticum	+	+
Rubus fruticosus	+	+
Rubus idaeus	-	+
Sorbus aucuparia	-	+
Teucrium scorodonia	-	+
Ulex gallii	-	+
Viola riviniana	+	-
Total no. of species	6	31

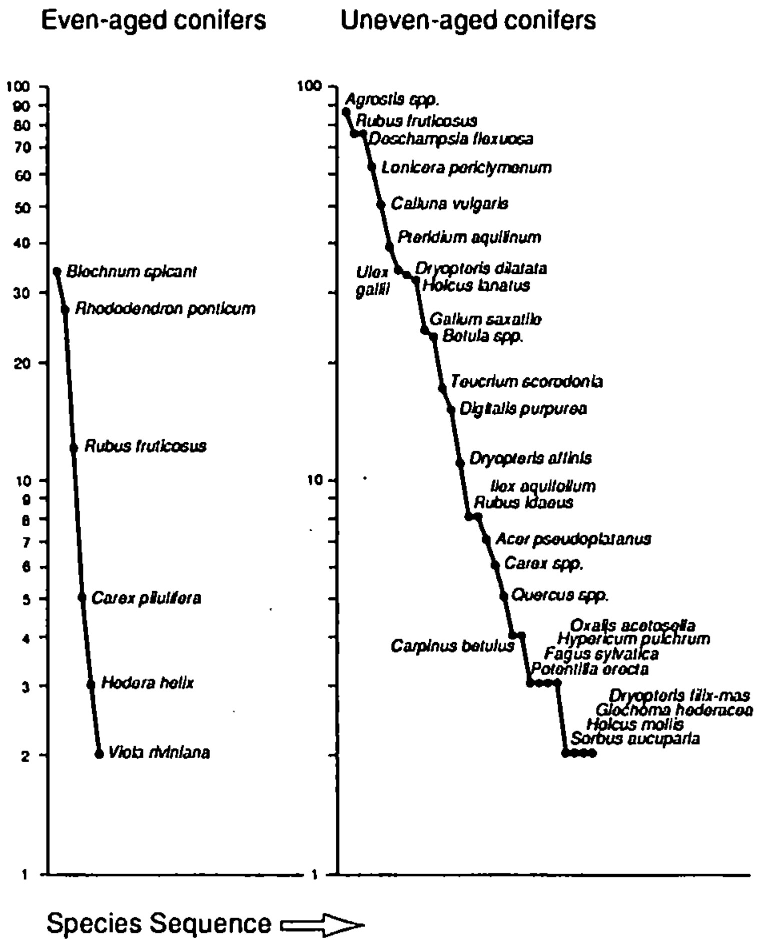


Figure 4.10a. Rank/abundance plot. Longleat Estate. Conifer stands. Ground flora species

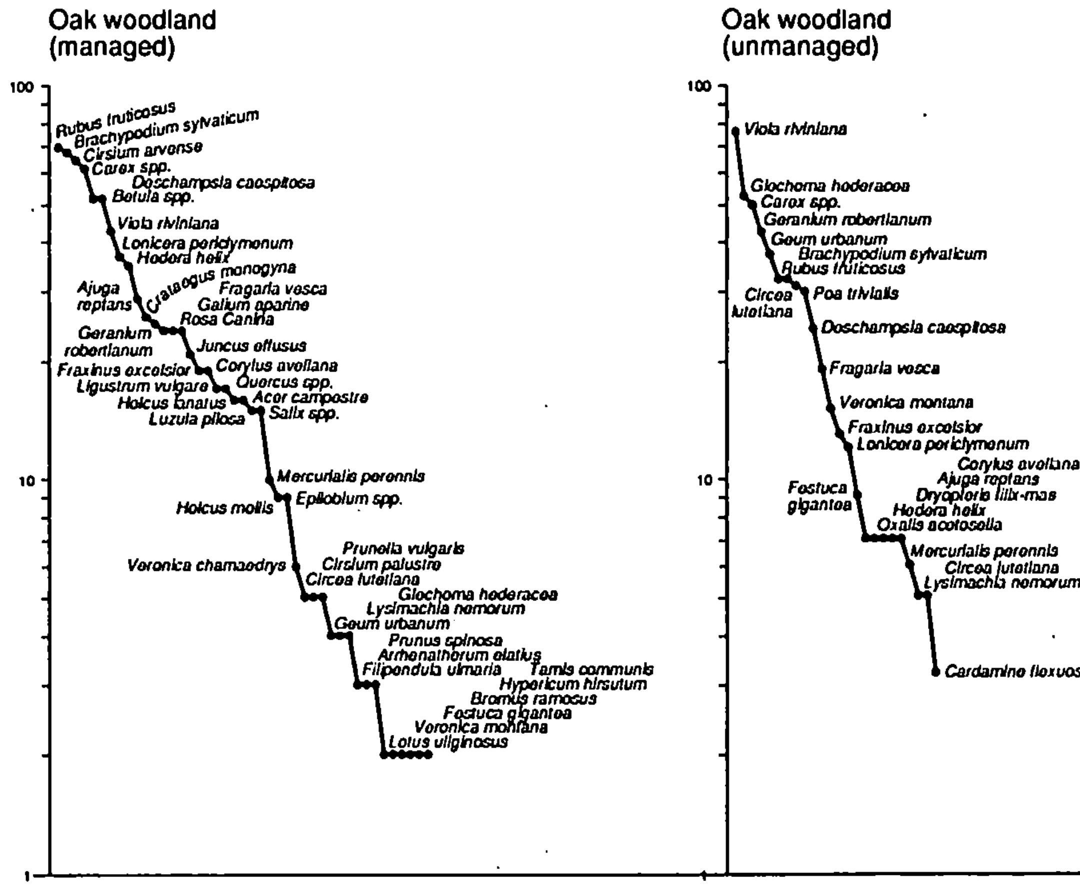


Figure 4.10b. Rank/abundance plot. Longleat Estate. Oak stands. Ground flora species

Table 4.15b. Number of seedlings in germination tests in even-aged and uneven-aged conifers on the Longleat Estate (Phase I sampling).

Species	Even-aged conifers		Uneven-aged conifers	
	i	ii	i	ii
Agrostis spp.	31	1	20	110
Calluna vulgaris	28	-	28	1
Carex spp.	189	-	22	4
Digitalis purpurea	-	-	2	-
Galium saxatile	-	-	4	3
Holcus lanatus	2	-	2	1
Hypericum pulchrum	-	-	1	-
Juncus effusus	51	3	8	-
Luzula pilosa	-	-	1	-
Poa trivialis	-	2	2	4
Rubus fruticosus	5	-	1	1
Ulex gallii	-	-	11	3
Total no. of seeds	306	6	102	127
Seeds.m^{-2}	3060	60	1020	1270
Total no. of species	6	3	12	8

i Soil samples (0-5 cm)
ii Litter samples

Table 4.16a. Species in the ground flora in managed and unmanaged oak stands at Blackdog Wood on the Longleat Estate.

Species	Managed oak	Unmanaged oak
Acer campestre	+	-
Ajuga reptans	+	+
Arrhenatherum elatius	+	-
Betula pendula/pubescens	+	-
Brachypodium sylvaticum	+	+
Bromus ramosus	+	-
Cardamine flexuosa	+	+
Carex pendula	+	-
Carex remota	+	-
Carex strigosa	-	+
Carex sylvatica	+	+
Circaea lutetiana	+	+
Cirsium arvense	+	-
Cirsium palustre	+	-
Cirsium vulgare	-	+
Corylus avellana	+	+
Crataegus monogyna	+	-
Deschampsia caespitosa	+	+
Dryopteris filix-mas	-	+
Epilobium spp.	+	-
Festuca gigantea	+	+
Filipendula ulmaria	+	-
Fragaria vesca	+	-
Fraxinus excelsior	+	+
Galium aparine	+	-
Geranium robertianum	+	+
Geum urbanum	+	+
Glechoma hederacea	+	+
Hedera helix	+	+
Holcus lanatus	+	-
Holcus mollis	+	-
Hypericum hirsutum	+	-
Juncus effusus	+	-
Ligustrum vulgare	+	-
Lonicera periclymenum	+	+
Lotus uliginosus	+	-
Luzula spp.	+	-
Lysimachia nemorum	-	+
Mercurialis perennis	+	+
Moehringia trinervia	+	-
Oxalis acetosella	-	+
Poa trivialis	-	+
Potentilla sterilis	+	+
Prunella vulgaris	+	-
Prunus spinosa	+	-
Quercus spp.	+	-
Rosa canina	+	-
Rubus fruticosus	+	+
Salix spp.	+	-
Tamus communis	+	-
Veronica chamaedrys	+	-
Veronica montana	+	+
Viola riviniana	+	+
Total no. of species	47	25

Table 4.16b. shows the number of seedlings recorded in the germination tests from the soil and litter samples. The seed banks of the two stands appear to be similar.

4.3. CONCLUSION

In this chapter, the results of the phase I seed bank sampling and ground flora surveys have been presented. The poor germination from the phase I soil samples from two of the sites, the Tavistock and Longleat Estates, has already been referred to in section 3.4. Since this was thought to be due to unsuitable germination conditions in the shade tunnel, measures were taken to provide a more suitable germination environment for the phase II germination tests.

The amount of litter present at different sites was variable and the litter samples tended to dry out much more quickly than the soil samples. Few seeds germinated from the litter samples from any of the sites. For the phase II sampling, the litter sample was combined with the 0-5 cm depth sample and two additional depths (5-10 and 10-15 cm) were sampled, in order to study the depth distribution of seeds in the soil.

The results of the phase II seed bank sampling and ground flora surveys are presented in chapter five. Further surveys, of the seed rain and the seed banks and ground flora associated with rides, were carried out at the same time as the phase II sampling. These surveys are also described in chapter five.

Table 4.16b. Number of seedlings in germination tests in managed and unmanaged oak stands at Blackdog Wood on the Longleat Estate (Phase I sampling).

Species	Managed oak		Unmanaged oak	
	i	ii	i	ii
Agrostis spp.	2	29	13	-
Ajuga reptans	1	1	-	-
Brachypodium sylvaticum	-	1	1	1
Cardamine flexuosa	4	-	7	-
Carex spp.	8	25	12	4
Cirsium arvense	-	1	-	-
Galium aparine	-	2	-	-
Geranium robertianum	-	2	2	2
Glechoma hederacea	1	-	4	-
Holcus lanatus	-	5	-	-
Hypericum perforatum	1	-	-	-
Juncus effusus	68	21	106	-
Luzula sp.	4	1	-	-
Poa trivialis	62	54	57	427
Potentilla sterilis/Fragaria vesca	2	-	2	-
Rubus fruticosus	-	1	-	-
Veronica chamaedrys	2	-	-	-
Veronica montana	1	-	3	-
Total no. of seeds	156	143	207	434
Seeds.m^{-2}	1560	1430	2070	4340
Total no. of species	12	12	10	4

i Soil samples (0-5 cm)
ii Litter samples

CHAPTER FIVE : SEED BANK AND GROUND FLORA SURVEYS, SECOND YEAR (PHASE II) SAMPLING

5.1. INTRODUCTION

In this chapter the results of the phase II seed bank sampling and surveys are presented. Since this second phase of sampling was intended to extend the information already obtained, the phase II sampling was carried out at the same four sites as the phase I sampling and at one additional site, Yarner Wood on the south east margin of Dartmoor. This upland site was included for contrast with the other lowland sites. Yarner Wood has been described in section 3.3. and the location of the sampling plots shown in Figure 3.6. A ground flora survey was also carried out at this site.

The sampling methods used in the phase II survey have been described in section 3.4. One of the aims of the phase II sampling was to study the depth distribution of seeds in the soil and to build up a clearer picture of seed bank heterogeneity at the chosen study sites. This was particularly relevant for the two sites, the Tavistock Woodlands Estate and the Longleat Estate, where the numbers of seeds germinating from the phase I samples had been low. The results of the seed rain and ride surveys are also presented in this chapter.

5.2. RESULTS

5.2.1. Yarner Wood

Ground flora and seed bank survey

TWINSPAN was applied to the data from the ground flora survey. The TWINSPAN classification is shown in Table 5.1.; standard cut levels were used. The eight quadrat groupings can be regrouped into four groups, A & B, C, D and E, F, G & H. The DECORANA ordination plots for the canopy types and the TWINSPAN groups are shown in Figures 5.1a. and 5.1b. Groups A & B correspond to the cut coppice and are distinguished by the presence of *Calluna vulgaris*, a species associated with open conditions. Group C corresponds to the abandoned coppice and group D the oak woodland. These two groups have very similar species compositions, due to the similar conditions which exist beneath the two canopy types. *Vaccinium myrtillus* dominates the ground flora and other shade-tolerant species such as *Melampyrum pratense* and *Hedera helix* are present. Few other species are present. Groups E, F, G & H correspond to the birch woodland. The species diversity is higher than in groups C and D. *Vaccinium myrtillus* occurs less frequently and *Rubus fruticosus* and *Pteridium aquilinum* more frequently, due to the more open nature of the canopy. Mosses are abundant. Several species, such as *Lonicera periclymenum* and *Teucrium scorodonia*, occur exclusively in this group. Regenerating tree seedlings such as *Ilex aquifolium*, *Sorbus aucuparia*, *Quercus spp*. and *Betula pendula* occur in all groups.

Table 5.2a. shows the species present in the ground flora in the four canopy types and the rank/abundance plot is shown in Figure 5.2. The ground flora diversity at this site

quadrats

```
                 77677666676766745844445556144555 1126 14551114   5     117771433223322332322333 22
                 26903143745568182024693690517045303024437818951261578927789600145493938871656227

   13 BARE SOIL  322224432152244------------------222-3---------3-------------------------2-2-------4-   0000
   17 STUM       43-4---------3-433-----------------------------------------------2----------------4   0000
    2 CALL VULG  -----2455534422--4---------------------------------------------------------------   0001
    3 CARE PILU  --22---2-------------------------------------------------------------------------   0001
    9 DESC FLEX  2--34----------------------------------------------------------------------------   0001
   18 VACC MYRT  55555555555555555555555555555555555555555555555555555555555554--434--5-------------   001
   14 LEAF LITT  5-5554454444455555555555555555555555555555555555555555555555555555555555555555555   010
   16 LOGS       -32---------4333-2--2221---232-331-2-1-2-2--2221----322222525----2-22----2244234-   010
    6 MELA PRAT  3232222122 1-222--4---2----1--1--32122222222422432222221232222 2-1-12222332---12-   011
   10 SORB AUCU  --------------453-----------------------2-22-33--2-243344----------3122-3-------2   011
   12 ILEX AQUI  ------4--------------------------32-------2------------------2---------2---------2-   011
    1 PTER AQUI  ----324435-34242-2434343-34-2-2-------3----323------------333445554554543444355 54   10
    4 HEDE HELI  334432234534432-------------3-----2222232---223-322-4232232332354322345424544435 44   10
   11 QUER SPP   ----------------23------3-----------------2----11----------3-22--23-------22--------   10
   19 BETU PEND  22---2--------1----------------------------------------------------------------2-4   10
    5 LONI PERI  -------------------------------------------------------------33223-3322243244-23   11
    7 RUBU FRUT  ----------------------------------223------333------------4---33334232444543334334 4   11
    8 TEUC SCOR  -------------------------------------------------------------22-333-22-2--2----2   11
   15 MOSS       22---2-23-2-34-332--33--221-----11------------22-23234-35-2154442324443535435355   11

                 00000000000000000000000000000000000000000000000000000000000000111111111111111111111
                 00000000000000011111111111111111111111111111111111111111111111000000001111111111111
                 00000111111111100000000000000000011111111111111111111111111111000111111000000000001
                 00111000000001110011111111111111110000000000000011111111111111 001111000000011111
                      0000011        011111111111111100000000001111000000000000011    00001100000 1
                      00111           00000000111111 0000011111     00001111111            00001

       groups      A       B              C                       D                E    F        G     H
```

Key

% cover	abundance
0	-
1 - 2	1
3 - 5	2
6 - 10	3
11 - 20	4
> 20	5

Table 5.1. TWINSPAN classification of ground flora data from abandoned coppice, cut coppice, oak and birch woodland at Yarner Wood.

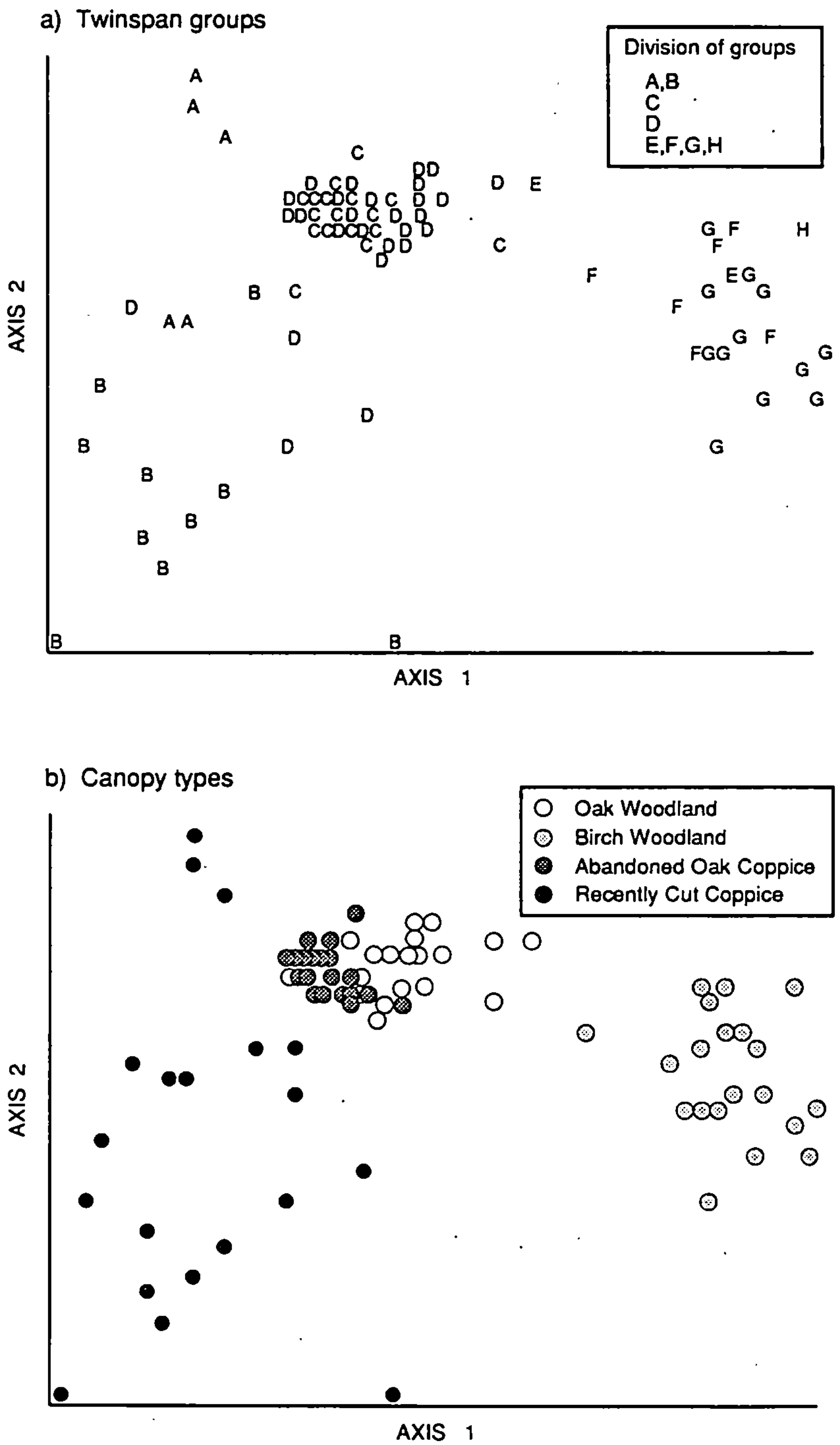


Figure 5.1. DECORANA ordination plots - ground flora survey
Phase I sampling : Yarner Wood

Table 5.2a. Species in the ground flora at Yarner Wood.

Species	Cut coppice	Abandoned coppice	Birch wood	Oak wood
Betula pendula	+	-	+	-
Calluna vulgaris	+	-	-	-
Carex pilulifera	+	-	-	-
Deschampsia flexuosa	+	-	-	-
Hedera helix	+	-	+	+
Ilex aquifolium	+	-	+	+
Lonicera periclymenum	-	-	+	-
Melampyrum pratense	+	+	+	+
Pteridium aquilinum	+	+	+	+
Quercus petraea	+	+	+	+
Rubus fruticosus	-	-	+	+
Sorbus aucuparia	+	+	+	+
Teucrium scorodonia	-	-	+	-
Vaccinium myrtillus	+	+	+	+
Total no. of species	11	5	11	8

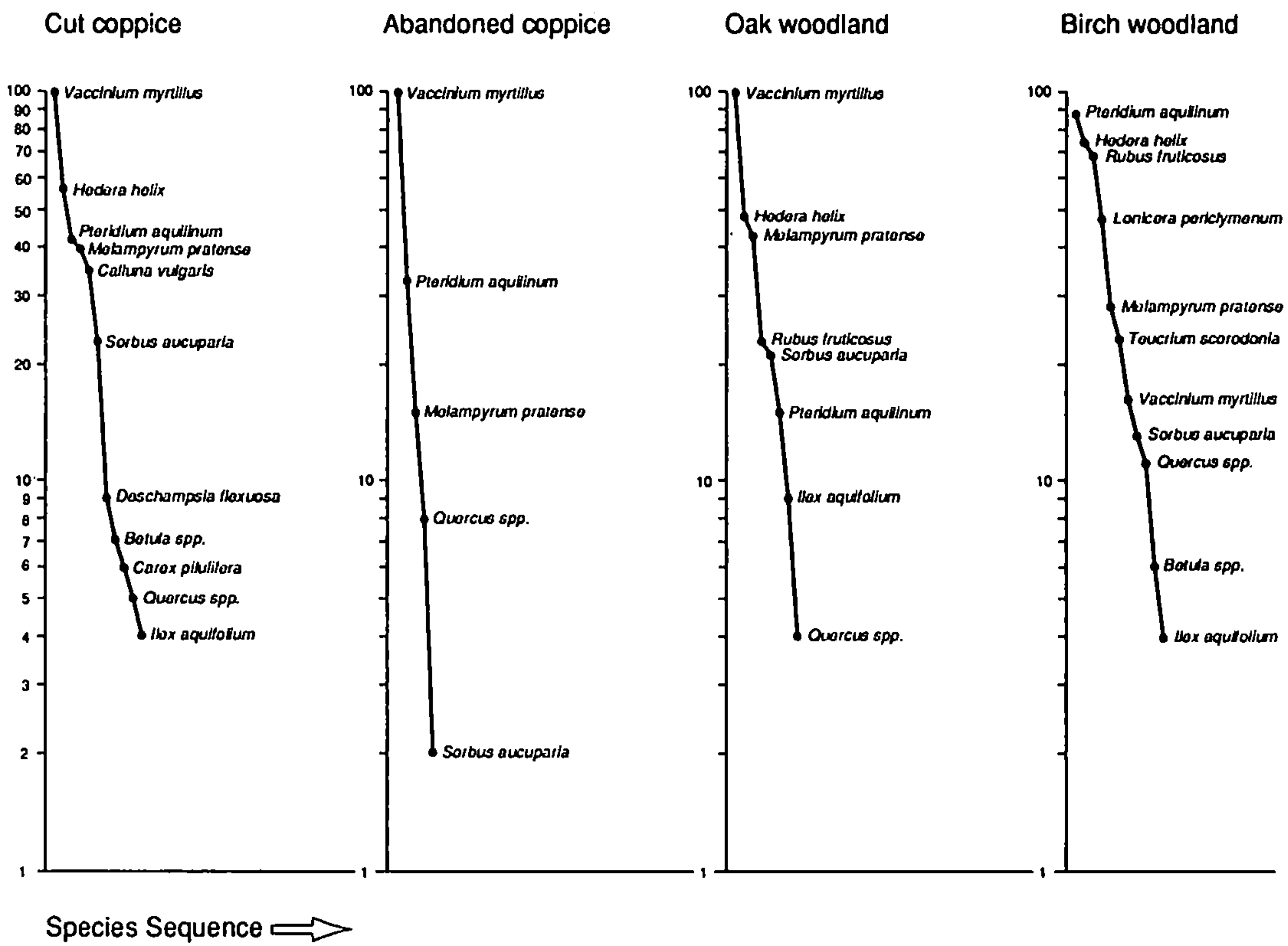


Figure 5.2 Rank/abundance plot. Yarner Wood. Ground flora species

is very limited. Only eleven species were recorded in the most diverse birch woodland and cut coppice plots and only five species in the least diverse abandoned coppice plot. *Vaccinium myrtillus* dominates the ground flora on all plots except the birch woodland where *Pteridium aquilinum* and *Rubus fruticosus* are more abundant. *Calluna vulgaris* has increased its cover on the re-coppiced plot and *Deschampsia flexuosa*, a species characteristic of woodland clearings, is present only on this plot.

The seed banks at this site are species-poor, as shown in Table 5.2b. In the cut coppice plot, the seed bank is dominated by *Calluna vulgaris*. This is the only plot where high seed densities were recorded. In the three other sample plots, abandoned coppice, birch woodland and oak woodland, seed densities were much lower. Fewer *Calluna* seeds are present in these plots; the most abundant species in the seed banks are *Betula pendula* and/or *Vaccinium myrtillus*.

Betula seeds are most abundant in the birch woodland and abandoned coppice plots. *Vaccinium* seeds are most abundant in the seed bank of the oak woodland and abandoned coppice plots. The seeds of both species are concentrated in the 0-5 cm layer, but are also present lower down the profile, in both the 5-10 and 10-15 cm layers, particularly in the abandoned coppice. *Vaccinium* seeds are much less abundant or absent from the seed banks of the cut coppice and birch woodland respectively.

Calluna seeds are most common in the seed bank of the cut coppice, being abundant in all three soil layers. Fewer seeds of *Calluna vulgaris* are present in the seed banks

Table 5.2b. Species in the seed bank at Yarner Wood (Phase II sampling).

Species	Cut coppice			Abandoned coppice		
	a	b	c	a	b	c
Betula pendula	31	3	3	119	42	28
Calluna vulgaris	565	1824	760	4	165	172
Carex pilulifera	-	2	8	-	-	3
Juncus effusus	2	1	1	3	-	-
Poa annua	3	-	1	-	-	-
Rubus fruticosus	-	1	1	1	1	-
Rumex acetosa	-	-	1	1	2	1
Vaccinium myrtillus	14	7	4	90	25	24
Total no. of seeds	615	1838	779	218	235	228
Seeds.m^{-2}	12300	36760	15580	4360	4700	4560
Total no. of species	5	6	8	6	5	5

Species	Birch woodland			Oak woodland		
	a	b	c	a	b	c
Betula pendula	124	18	11	20	1	1
Calluna vulgaris	7	13	15	2	40	20
Carex pilulifera	-	-	-	-	2	-
Chamaenerion angustifolium	-	-	-	1	-	-
Juncus effusus	1	2	-	1	-	1
Luzula pilosa	1	1	-	-	-	-
Poa annua	-	1	1	-	-	-
Rubus fruticosus	21	17	11	4	3	2
Rumex acetosa	-	-	-	-	1	-
Vaccinium myrtillus	-	-	-	117	11	6
Total no. of seeds	154	52	38	145	58	30
Seeds.m^{-2}	3080	1040	760	2900	1160	600
Total no. of species	5	6	4	6	6	4

Key to soil depths
a 0-5 cm
b 5-10 cm
c 10-15 cm

of the other three canopy types and are more concentrated in the 5-10 and 10-15 cm layers.

Other species present in the seed banks include *Juncus effusus*, *Carex pilulifera*, *Luzula pilosa*, *Poa annua*, *Rumex acetosa*, *Rubus fruticosus* and *Chamaenerion angustifolium*. Some of these species were not recorded in the ground flora survey, although those which were absent from the sample plots were generally present in nearby clearings and rides.

The data described above illustrate how the depth distribution of seeds of different species in the soil can change as a result of changes in the canopy. Such changes, associated with various forms of woodland management, affect the ground flora and consequently the seed bank. In this case, the re-coppicing treatment has noticeably influenced the vertical distribution of seeds of *Calluna vulgaris* in the soil.

5.2.2. Tavistock Woodlands and Longleat Estate

Tavistock Woodlands Estate: Seed bank survey

Table 5.3. shows the species in the seed bank of the Bradford Plan sub-units (I-V). Seed densities generally decrease with depth in the soil, although the distributions of different species vary and in some cases higher concentrations of seeds occur at lower depths.

Seed bank densities are greater in the younger sub-units (IV and V) than in older sub-units (I, II and III). This is mainly due to an abundance of *Juncus* seeds, although

Table 5.3. Species in the seed bank of a Bradford Plan unit at Grenoven Wood on the Tavistock Woodlands Estate (Phase II sampling). I-V represent B-Plan stages.

Species	I 27 yrs			II 21 yrs			III 15 yrs			IV 9 yrs			V 3 yrs		
	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
Agrostis spp.	-	2	-	-	-	-	-	-	-	-	-	-	45	4	2
Betula spp.	8	-	-	5	-	-	2	-	-	-	-	-	1	-	-
Calluna vulgaris	19	4	7	32	23	5	-	-	-	46	40	9	4	1	3
Carex pilulifera	4	2	-	1	2	4	2	1	-	8	11	-	2	1	-
Digitalis purpurea	2	-	-	-	-	-	-	-	-	8	13	7	82	8	-
Hypericum pulchrum	5	8	9	11	19	2	-	8	2	17	42	37	23	40	13
Juncus effusus	3	1	3	1	-	-	1	1	-	104	82	24	312	47	10
Luzula pilosa	2	-	1	1	1	-	1	-	-	-	-	4	5	3	3
Rubus fruticosus	7	1	-	3	-	4	5	-	-	-	1	1	6	1	-
Teucrium scorodonia	-	-	-	-	-	-	-	-	-	2	2	-	1	-	-
Ulex gallii	-	-	-	-	-	-	-	-	1	2	-	1	-	-	-
Veronica chamaedrys	-	-	-	-	-	-	-	-	-	-	-	-	8	1	2
Veronica officinalis	-	-	-	-	-	-	-	-	-	-	-	-	30	20	6
Total no. of seeds	50	18	20	54	45	15	11	10	3	187	191	83	519	126	39
Seeds.m^{-2}	5000	1800	2000	5400	4500	1500	1100	1000	3000	18700	19100	8300	51900	12600	3900
Total no. of species	8	6	4	7	4	4	5	3	2	7	7	7	12	10	7

Key to soil depths
a 0-5 cm
b 5-10 cm
c 10-15 cm

there are also higher numbers of seeds of *Agrostis*, *Veronica*, *Teucrium*, *Digitalis* and *Hypericum*. These are all species which become more abundant in the ground flora of cleared sub-units.

Table 5.4. shows the species in the seed bank of the abandoned and recently cut coppice. Few species other than *Calluna vulgaris* are present in the seed banks. Seed densities show the familiar trend of decline with depth in the soil. Seed densities are higher in the abandoned coppice than in the cut coppice. *Calluna vulgaris* was present in the ground flora beneath the incomplete canopy of the abandoned coppice at this site, accounting for the very high densities of *Calluna* seeds in the soil.

Longleat Estate: Seed bank survey

Table 5.5. shows the species in the seed bank of the even-aged and uneven-aged conifer stands. The results from the phase II samples do not support the tentative conclusion from the phase I results that there were fewer species in the seed bank of the even-aged plantation than in the uneven-aged stand. Most of the species in the seed banks occur beneath both canopy types but often at low densities. *Calluna vulgaris* occurs at high densities in both stands and *Carex pilulifera* and *Juncus effusus* at high densities in the even-aged stand. The two former species were recorded in the ground flora of the uneven-aged stand, but were absent or poorly represented in the even-aged stand. All three species are likely to have been abundant in the even-aged stand before canopy closure and all have seeds which are long-lived in the soil. *Juncus effusus* was not recorded in the ground flora of the uneven-aged stand and was not abundant in the seed bank, which suggests that it has never been abundant in the ground flora of this stand. In the uneven-aged stand, the abundance

Table 5.4. Species in the seed bank in cut and abandoned coppice at Blanchdown Wood on the Tavistock Woodlands Estate (Phase II sampling).

Species	Cut coppice			Abandoned coppice		
	a	b	c	a	b	c
Agrostis capillaris	1	-	-	1	-	-
Betula spp.	6	-	-	25	2	-
Calluna vulgaris	62	73	17	860	496	197
Carex pilulifera	-	-	1	-	1	-
Poa annua	1	-	-	1	1	-
Rubus fruticosus	-	1	-	16	5	2
Rumex obtusifolius	-	-	-	-	1	2
Ulex gallii	-	-	-	-	-	2
Vaccinium myrtillus	-	-	-	3	-	1
Total no. of seeds	70	74	18	906	506	204
Seeds.m^{-2}	1400	1480	360	18120	10120	4080
Total no. of species	4	2	2	6	6	5

Key to soil depths
a 0-5 cm
b 5-10 cm
c 10-15 cm

Table 5.5. Species in the seed bank in even-aged and uneven-aged conifers on the Longleat Estate (Phase II sampling).

Species	Even-aged conifers			Uneven-aged conifers		
	a	b	c	a	b	c
Agrostis spp.	18	13	7	204	30	31
Betula spp.	-	-	-	3	1	1
Calluna vulgaris	1119	671	299	866	243	105
Carex spp.	103	10	1	8	6	9
Digitalis purpurea	6	-	-	-	-	-
Galium saxatile	-	-	-	3	-	-
Holcus lanatus	1	-	-	-	-	-
Hypericum pulchrum	2	1	-	17	29	39
Juncus effusus	517	213	232	11	4	3
Lotus corniculatus	-	-	-	-	8	1
Poa trivialis	-	-	-	1	14	-
Potentilla erecta	-	-	-	-	1	-
Rubus fruticosus	27	3	7	28	6	8
Rumex acetosa	-	-	2	-	2	1
Teucrium scorodonia	5	3	2	-	-	-
Ulex gallii	1	-	-	10	33	15
Veronica montana	-	-	2	-	-	-
Total no. of seeds	1799	914	522	1151	387	213
Seeds.m^{-2}	35980	18280	11040	23020	7740	4260
Total no. of species	10	7	8	10	12	10

Key to soil depths
a 0-5 cm
b 5-10 cm
c 10-15 cm

of seeds of *Agrostis spp.* in the upper soil layer reflects the abundance of this species in the ground flora. Other than this, the relatively short period of time that the two plots have been managed differently (less than 20 years) is insufficient to allow very much divergence of the seed banks. Seed densities in both stands declined with depth.

Table 5.6. shows the species in the seed banks of the oak stands at Blackdog Wood. The lower species diversity of the ground flora in the unmanaged stand was not associated with a significantly lower seed bank diversity. Several species were found only in the seed bank of the managed stand, for example *Cirsium spp.*, *Holcus lanatus* and *Glechoma hederacea*, but otherwise the seed banks in the two stands were similar. The only species present in both stands at high densities was *Juncus effusus*. High densities of this species in the lower soil layers in both stands reversed the usual trend for decline in seed density with depth. High densities of *Poa trivialis* and *Hypericum spp.* were present in the seed bank of the unmanaged stand.

5.2.3. Werrington Park and Lindridge Estates

Werrington Park Estate: Seed bank survey

Tables 5.7. and 5.8. show the numbers of seedlings recorded in the germination tests. In the two youngest conifer plantations very high seed densities occurred. *Juncus effusus* was by far the most abundant species in the seed banks. Other species which were frequent in the seed banks were *Digitalis purpurea* and *Rubus fruticosus*. The seed densities in the three older plantations were lower and no one species predominated. Species common in the seed banks were *Calluna vulgaris*, *Juncus effusus*, *Carex pilulifera* and *Galium saxatile*. The lowest seed density occurred in the

Table 5.6. Species in the seed bank in managed and unmanaged oak stands at Blackdog Wood on the Longleat Estate (Phase II sampling).

Species	Managed oak			Unmanaged oak		
	a	b	c	a	b	c
Agrostis spp.	2	2	-	3	-	-
Ajuga reptans	-	-	-	2	-	-
Betula spp.	2	2	-	6	2	-
Cardamine flexuosa	3	-	-	14	1	4
Carex spp.	9	-	6	21	4	-
Cerastium fontanum	-	-	-	4	1	-
Chamaenerion angustifolium	-	-	-	2	1	-
Cirsium arvense	1	-	-	-	-	-
Cirsium palustre	2	-	-	-	-	-
Cirsium vulgare	2	-	-	-	-	-
Deschampsia caespitosa	1	-	-	-	-	-
Galium aparine	1	-	-	-	-	-
Geum urbanum	-	-	-	2	1	-
Geranium robertianum	1	-	-	-	-	-
Glechoma hederacea	12	1	1	-	-	-
Holcus lanatus	34	2	2	-	-	-
Hypericum perforatum	1	1	-	57	64	77
Juncus effusus	532	915	857	346	523	724
Luzula sp.	-	2	-	-	-	-
Lysimachia nemorum	-	-	-	6	5	2
Moehringia trinervia	7	3	2	-	-	-
Poa trivialis	1	4	-	56	22	8
Potentilla sterilis/F. vesca	5	1	3	14	2	-
Primula vulgaris	-	-	-	4	-	1
Rubus fruticosus	3	2	1	5	3	2
Rumex acetosa	-	-	-	-	1	-
Scrophularia auriculata	-	-	1	2	2	4
Veronica chamaedrys	18	14	5	-	-	-
Veronica montana	3	1	-	2	1	2
Viola riviniana	1	-	-	-	-	-
Total no. of seeds	641	950	877	546	633	824
Seeds.m^{-2}	12820	19000	17540	10920	12660	16480
Total no. of species	21	13	9	17	15	9

Key to soil depths
a 0-5 cm
b 5-10 cm
c 10-15 cm

Table 5.7. Species in the seed bank in young conifer plantations at the Werrington Park Estate (Phase II sampling).

Species	Sitka spruce 28 yrs			Sitka spruce 29 yrs		
	a	b	c	a	b	c
Agrostis spp.	7	6	4	1	1	-
Betula spp.	11	-	-	6	6	3
Carex pilulifera	1	2	6	26	4	1
Cerastium fontanum	2	-	-	-	-	-
Digitalis purpurea	52	99	66	260	42	5
Gnaphalium uliginosum	-	-	-	-	4	-
Hyacinthoides non-scripta	1	-	-	2	1	-
Hypericum pulchrum	-	-	1	-	-	-
Hypochoeris radicata	-	-	-	1	-	-
Juncus effusus	2842	1883	555	1347	653	245
Lotus corniculatus	-	-	-	29	11	9
Rubus fruticosus	61	10	1	46	6	4
Rumex acetosella	-	-	-	4	3	-
Rumex obtusifolius	2	1	-	-	-	-
Scrophularia auriculata	-	-	-	3	2	-
Silene dioica	8	-	-	21	3	1
Teucrium scorodonia	2	-	-	-	-	-
Ulex gallii	1	-	-	-	8	5
Total no. of seeds	2990	2001	635	1747	744	273
Seeds.m^{-2}	59800	40020	12700	34940	14880	5460
Total no. of species	12	6	5	13	13	8

Key to soil depths
a 0-5 cm
b 5-10 cm
c 10-15 cm

Table 5.8. Species in the seed bank in the older conifer plantations at the Werrington Park Estate (Phase II sampling).

Species	Sitka spruce 42 yrs			Japanese larch 42 yrs			European larch 53 yrs		
	a	b	c	a	b	c	a	b	c
Agrostis spp.	7	16	3	5	3	1	2	1	1
Betula spp.	3	3	-	1	-	-	2	2	-
Calluna vulgaris	308	253	55	248	103	31	6	10	15
Carex pilulifera	144	104	10	154	13	4	123	90	46
Digitalis purpurea	1	12	15	25	41	10	2	1	1
Galium saxatile	87	27	3	166	14	3	3	1	1
Hypericum pulchrum	5	11	3	2	6	13	-	-	-
Hyacinthoides non-scripta	-	-	-	-	-	-	-	-	-
Juncus effusus	38	52	20	59	182	59	1	1	-
Luzula pilosa	-	-	-	-	1	-	-	-	-
Poa annua	-	1	-	-	-	-	1	-	-
Potentilla erecta	4	7	-	-	-	1	-	-	-
Rubus fruticosus	20	8	1	16	3	1	29	15	4
Rumex acetosella	-	-	-	1	-	-	65	29	-
Silene dioica	-	-	-	-	-	-	5	2	-
Teucrium scorodonia	1	2	-	-	-	-	-	-	-
Ulex gallii	8	31	28	50	63	37	5	11	4
Total no. of seeds	626	527	138	727	429	160	246	163	7
Seeds.m^{-2}	12520	10540	2760	14540	8580	3200	4920	3260	1440
Total no. of species	12	13	9	11	10	10	13	11	7

Key to soil depths
a 0-5 cm
b 5-10 cm
c 10-15 cm

oldest plantation and the two most abundant species in the seed bank of this plantation were *Digitalis purpurea* and *Rumex acetosella*. In all five plantations, seed densities declined with depth.

<u>Lindridge Estate: Seed bank survey</u>

Tables 5.9. and 5.10. show the number of species recorded in the germination tests. The most common species in the seed bank of the larch plantation was *Hypericum perforatum*. No one species predominated in the seed bank of the Douglas fir plantation or the felled area. In the abandoned coppice, *Betula pendula* was the most abundant species. In all plots, seed densities declined with depth.

5.3. DEPTH DISTRIBUTION OF SEEDS IN THE SOIL

The depth distribution of seeds in the soil was examined by calculating the percentages of seeds in the three soil layers at each site, using combined data from all plots where phase II sampling was carried out (see Figure 5.3.). The density of seeds in the soil generally decreased with depth, as illustrated by the data from the Tavistock, Longleat, Werrington Park and Lindridge Estates. At Yarner Wood, there were more seeds in the 5-10 cm layer than in the 0-5 cm layer, mainly due to an abundance of *Calluna vulgaris* seeds in this layer in the abandoned coppice.

The depth distributions of seeds of the twelve most common genera were examined by calculating percentages of seeds in the three soil layers, using combined data from all sites where phase II sampling was carried out (Figure 5.4.). These depth distributions are not necessarily characteristic features of the species concerned.

Table 5.9. Species in the seed bank in conifer plantations at Buckley Wood on the Lindridge Estate (Phase II sampling).

Species	Douglas fir			Hybrid larch		
	a	b	c	a	b	c
Antirrhinum majus	1	1	1	-	-	-
Betula pendula	16	7	2	13	2	1
Buddleja davidii	-	-	-	1	-	-
Cardamine hirsuta	3	2	-	1	1	-
Carex spp.	4	1	-	3	-	-
Cirsium arvense	17	4	4	2	-	-
Cirsium vulgare	1	-	-	-	1	-
Clematis vitalba	-	-	-	1	-	-
Crataegus monogyna	-	-	-	-	1	-
Eupatorium cannabinum	1	-	-	2	-	-
Euphorbia amygdaloides	4	-	-	3	-	-
Fraxinus excelsior	1	-	-	-	-	-
Hypericum perforatum	12	1	-	107	65	1
Hypericum tetrapterum	-	-	-	4	2	2
Hypochoeris radicata	-	2	-	-	-	-
Iris foetidissima	2	2	-	1	1	-
Lapsana communis	-	-	-	-	1	2
Luzula sp.	-	1	-	-	-	-
Poa annua/trivialis	7	3	7	4	2	2
Primula vulgaris	1	1	1	4	1	2
Rubus fruticosus	28	7	4	7	1	-
Rumex acetosa	26	7	2	23	6	2
Scrophularia nodosa	-	2	-	1	2	-
Senecio jacobaea	-	1	-	-	-	-
Silene alba	-	-	-	1	2	-
Stachys sylvatica	-	-	-	3	1	-
Urtica dioica	65	27	17	37	24	17
Verbascum thapsus	3	2	3	-	-	1
Veronica chamaedrys	-	-	-	1	1	-
Veronica montana	2	1	1	-	-	-
Veronica persica	-	1	-	-	-	-
Viola riviniana	-	1	-	1	-	-
Total no. of seeds	194	74	42	220	114	30
Seeds.m^{-2}	3880	1480	840	4400	2280	600
Total no. of species	18	20	10	21	17	9

Key to soil depths
a 0-5 cm
b 5-10 cm
c 10-15 cm

Table 5.10. Species in the seed bank in the felled area and abandoned coppice at Buckley Wood on the Lindridge Estate (Phase II sampling).

Species	Felled area			Abandoned coppice		
	a	b	c	a	b	c
Agrostis spp.	-	1	-	-	-	-
Ajuga reptans	-	-	-	2	-	-
Betula pendula	8	5	2	64	24	8
Buddleja davidii	-	2	-	-	-	-
Carex spp.	-	-	-	-	1	-
Centaurium erythraea	-	-	-	-	1	-
Cerastium fontanum	3	-	-	-	-	-
Chamaenerion angustifolium	1	-	-	-	-	-
Cirsium arvense	2	-	1	1	2	-
Cirsium vulgare	30	2	6	2	-	-
Clematis vitalba	-	-	-	1	-	1
Crataegus monogyna	-	-	-	-	1	-
Eupatorium cannabinum	-	1	-	-	-	-
Euphorbia amygdaloides	2	-	-	-	-	-
Fraxinus excelsior	-	-	-	2	-	-
Hypericum hirsutum	2	1	-	-	-	-
Hypericum perforatum	7	23	19	-	10	14
Lapsana communis	-	1	-	-	-	-
Myosotis arvensis	1	-	-	-	-	-
Poa annua/trivialis	2	-	1	-	-	-
Potentilla sterilis	-	1	-	-	2	3
Primula vulgaris	-	-	2	1	2	2
Ranunculus repens	1	3	-	-	-	-
Rubus fruticosus	1	5	4	15	3	4
Rumex acetosa	-	-	3	1	-	-
Sambucus nigra	1	-	-	-	-	-
Senecio jacobaea	-	1	-	-	-	-
Silene alba	2	1	-	-	-	-
Stachys sylvatica	6	-	-	-	-	-
Urtica dioica	2	1	3	6	1	-
Verbascum thapsus	-	-	-	-	-	1
Veronica chamaedrys	1	2	1	-	2	2
Veronica montana	-	2	2	-	-	-
Veronica officinalis	-	-	-	1	-	-
Total no. of seeds	72	51	44	96	49	35
Seeds.m^{-2}	1800	1020	880	1920	980	700
Total no. of species	17	16	11	11	11	8

Key to soil depths
a 0-5 cm
b 5-10 cm
c 10-15 cm

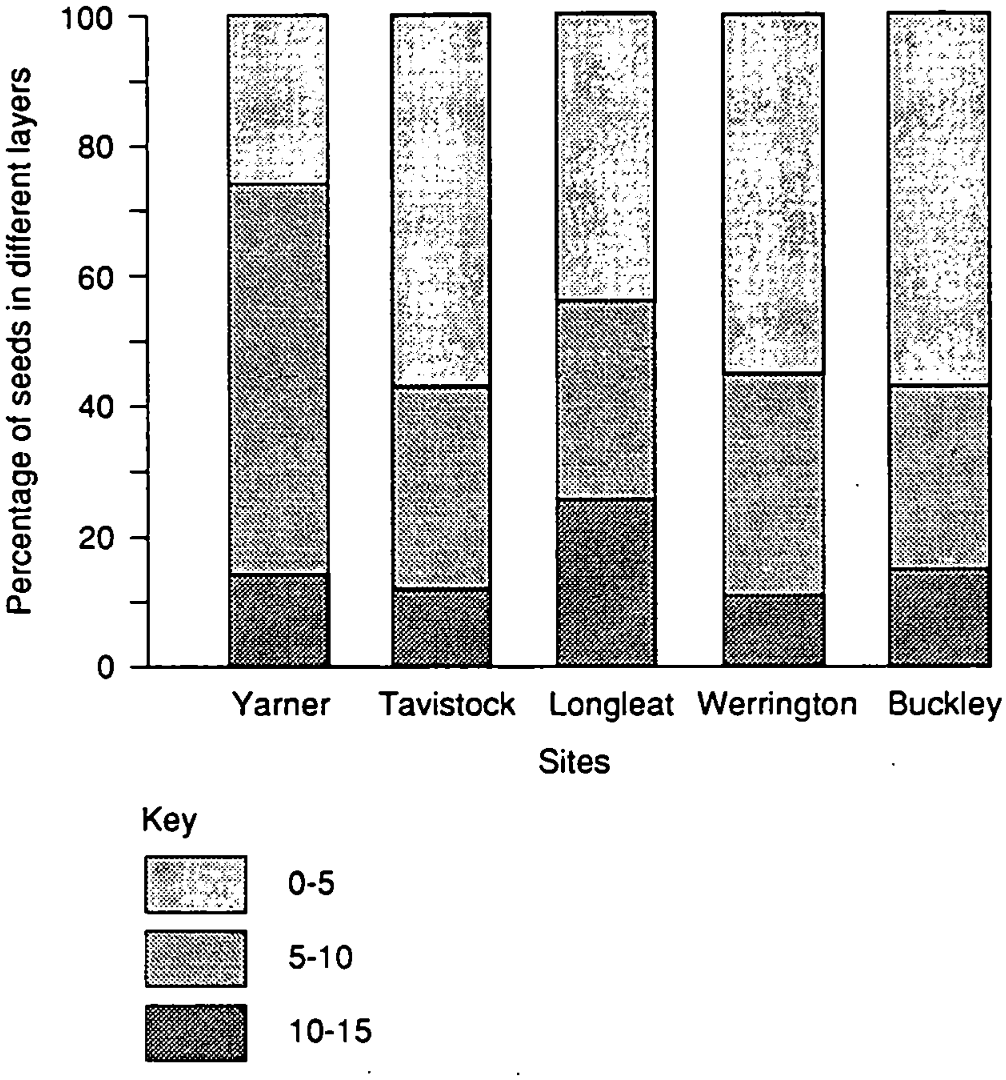


Figure 5.3. Phase II sampling data : Distribution of seeds in the three soil layers (percentage values) at the five study sites

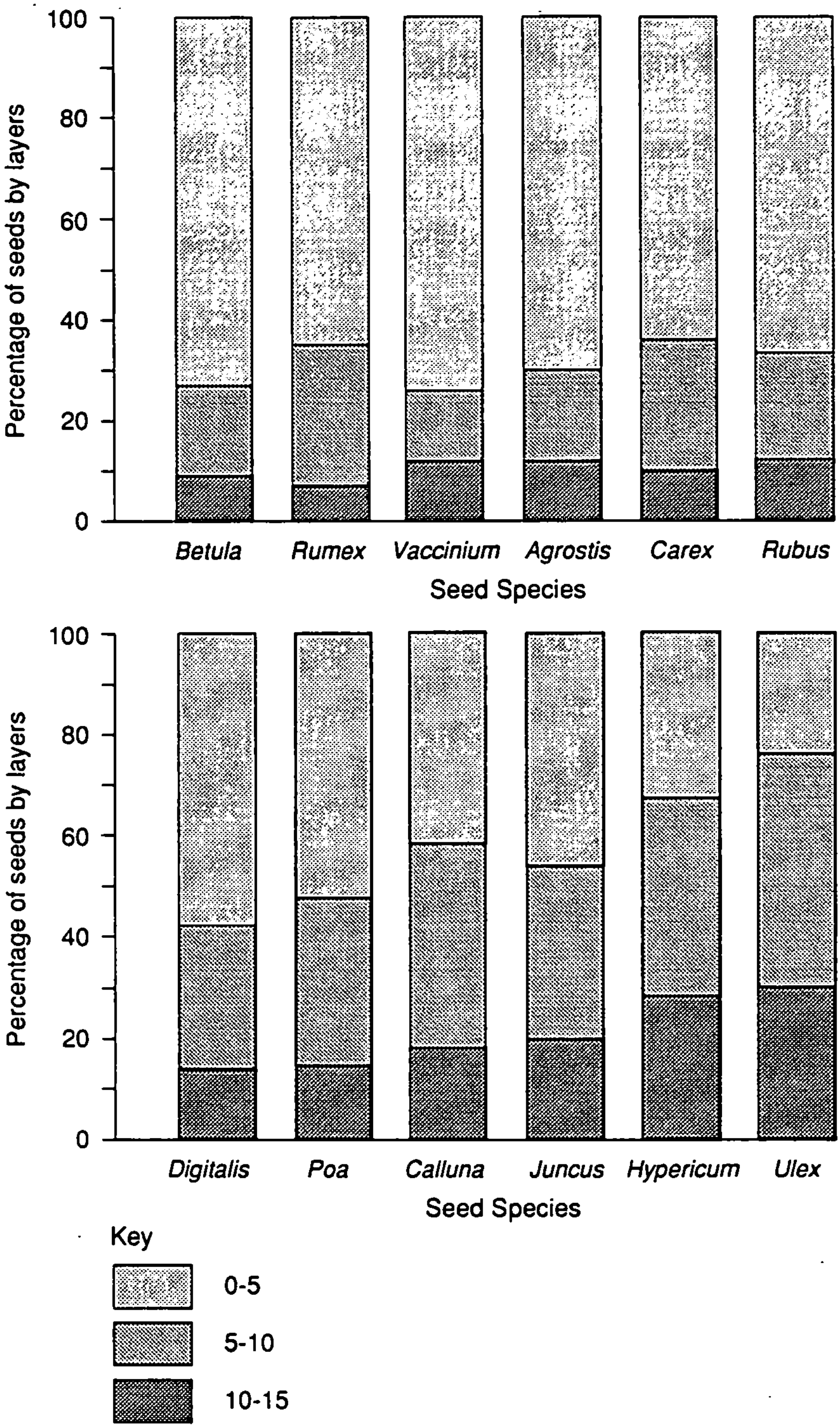


Figure 5.4 . Phase II sampling data : Distribution of seeds of different species in the three soil layers (percentage values)

Deeply buried seeds are assumed to be older than those in the top soil layers. Viable short-lived seeds are always more abundant in the surface soil, but long-lived seeds might be too, depending on the recent history of the site. Seeds of *Betula*, *Rumex*, *Vaccinium*, *Agrostis*, *Carex*, *Rubus*, *Digitalis* and *Poa* all had markedly higher concentrations in the top (0-5 cm) soil layer. Few seeds were recorded in the phase I litter data, but both *Betula* and *Agrostis* seeds were frequently present and sometimes occurred at high densities. It is notable that *Betula spp.*, *Rumex acetosella*, *Vaccinium myrtillus* and *Agrostis spp.* were amongst the species found by Hill & Stevens (1981) to be more concentrated in the litter and upper (0-5 cm) soil layer of upland conifer plantations. The seeds of these four species are generally considered to be relatively short-lived, *Vaccinium* and *Betula* much more so than the other two. However, the evidence for the survival of seeds of *Betula* and *Vaccinium* in the soil is conflicting. Granstrom (1987) found that seeds of both *Betula pendula* and *Vaccinium myrtillus* were viable after five years of burial in the soil of a Swedish coniferous forest. However, these seeds were placed in the soil for the purposes of the experiment. In natural conditions, losses due to germination and predation may be greater for seeds on, or near, the soil surface. When seeds of *Betula pendula* and *B. pubescens* were sown onto the moss carpet of a mature forest (Granstrom & Fries, 1985), the depletion rate was very high during the first year.

In contrast to other tree seeds, *Betula* seeds were often abundant in the soil samples. Although the seeds were most abundant in the 0-5 cm layer, they were present in both the 5-10 and 10-15 cm layers. Other studies (Brown & Oosterhuis, 1981; Hill & Stevens, 1981; Piroznikow, 1983; Granstrom, 1982, 1988; Staaf et al., 1987) have also recorded *Betula* seeds in forest soils. *Betula* seeds, unlike many other tree seeds, are small, readily dispersed and easily buried.

The presence of *Vaccinium myrtillus* seeds in both the 5-10 cm and 10-15 cm soil layers in this study suggests that the seeds, if they become buried, may be able to survive for some time in the soil. Several Russian studies have reported that seeds of *Vaccinium myrtillus* are absent or rare in the seed banks of forest soils, despite the presence of the species in the ground flora (Karpov, 1960; Petrov, 1977). Viable seeds of *Vaccinium myrtillus* were found in the 0-5 cm soil layer in Swedish conifer forests (Granstrom, 1982) and in conifer plantations in Britain (Hill & Stevens, 1981), but were absent from the 5-10 cm layer.

A number of studies indicate that the seeds of *Poa spp.*, *Rumex acetosella*, *Agrostis spp.*, and *Rubus spp.*, although not exceptionally long-lived, can survive for considerable periods of time in the soil. *Poa* seeds probably remain viable for less than five years. The seeds of *Rumex acetosella* appear to survive for 10 to 20 years and those of *Agrostis spp.* for 30 to 40 years (Hill & Stevens, 1981). The upper limit for survival of *Rubus* seeds is probably about 50 years (Marks, 1974; Graber & Thompson, 1978).

At most sites, large numbers of seeds of both *Calluna* and *Juncus* were present in the 0-5 cm layer. However, *Calluna* seeds were abundant in the 5-10 cm layer at Yarner Wood in the abandoned coppice and oak woodland and large numbers of *Juncus* seeds in this layer in the Longleat oak stands. The implication is that these more deeply buried seeds have been present for a long period of time beneath these canopies.

Since these species are absent from the ground flora, there has been no recent input of seed and there has been a decline in the numbers of seeds present in the top soil layer.

Ulex and *Hypericum* were the only two genera for which more seeds were recorded in the 5-10 cm layer than the 0-5 cm layer. These species were only recorded in the ground flora of the open sites and were never dominant species in the ground flora. The seeds tended to be more abundant in the lower soil layers at all the sites.

The seeds of *Carex spp., Digitalis purpurea, Calluna vulgaris, Juncus spp., Ulex spp.* and *Hypericum spp.* are generally considered to be long-lived. The results of a number of studies suggest that seeds of these species can survive in the soil for periods of longer than 50 years (Hill, 1986; Granstrom, 1988; Darby, 1987).

5.4. SEED RAIN SURVEY

The seed rain survey was carried out at three of the sites, the Tavistock Woodlands, Werrington Park and Lindridge Estates. Seed inputs were measured over a period of six months, from early spring to late autumn. The results of the survey are shown in Table 5.11.

The species composition of the seed rain can be compared with that of the seed bank and ground flora at each of the sites by referring to the appropriate tables and figures in chapter four. A number of tree seeds were present in the seed rain, including *Fraxinus excelsior, Quercus spp.* and *Picea sitchensis.* These trees were all growing

Table 5.11. Species recorded in the seed rain survey.

Species	Werrington Woods			Buckley Wood			Tavistock Woodlands		
	a	b	c	a	b	c	a	b	c
Agrostis capillaris	-	-	-	-	-	-	5	-	-
Betula spp.	2	3	2	6	8	9	7	9	8
Calluna vulgaris	1	3	1	-	-	-	1	1	4
Carex spp.	-	-	1	-	-	1	-	1	2
Cerastium fontanum	-	-	4	-	-	-	-	-	-
Chamaenerion angustifolium	1	2	-	-	-	2	-	-	6
Cirsium arvense	-	-	-	-	-	2	-	-	-
Digitalis purpurea	4	2	5	-	-	-	-	-	-
Euphorbia amygdaloides	-	-	-	1	4	-	-	-	-
Fraxinus excelsior	-	-	-	-	3	-	-	-	-
Galium aparine	-	-	-	7	-	-	-	-	-
Holcus lanatus	1	-	-	-	-	-	-	-	-
Hyacinthoides non-scripta	-	6	-	-	-	-	-	-	-
Hypericum pulchrum	-	1	-	-	-	-	-	-	-
Hypochoeris radicata	-	-	-	-	-	1	-	-	-
Iris foetidissima	-	-	-	6	-	-	-	-	-
Juncus effusus	3	4	2	-	-	-	1	-	-
Lapsana communis	-	1	1	1	-	-	-	-	-
Picea sitchensis	-	1	-	-	-	-	-	-	-
Poa annua/trivialis	-	-	4	5	-	-	-	1	-
Quercus spp.	-	-	-	-	-	-	2	-	-
Rubus fruticosus	9	-	1	3	-	-	-	1	3
Rumex obtusifolius	-	1	2	-	-	-	-	-	-
Silene dioica	-	9	7	-	-	-	-	-	-
Urtica dioica	1	-	1	7	-	-	-	-	-
Total no. of seeds	22	23	31	49	11	15	16	13	23
Seeds.m^{-2}	88	132	124	196	44	60	64	52	92
Total no. of species	8	11	12	8	2	3	5	5	5

Key to canopy types

Werrington Woods	Buckley Wood	Tavistock Woodlands
a Japanese larch 42 yrs	a Felled area	a Cut coppice
b Sitka spruce 42 yrs	b Abandoned coppice	b Abandoned coppice
c Sitka spruce 28 yrs	c Hybrid larch	c B-Plan unit

at the sites, their seeds are short-lived and were absent from the seed banks. Other large-seeded species with transient seed banks, such as *Hyacinthoides non-scripta*, *Euphorbia amygdaloides*, *Galium aparine* and *Iris foetidissima* were also only recorded in the seed rain at sites where they were present in the ground flora. Large seeds tend be poorly dispersed unless they have specialised dispersal mechanisms. The seeds of many forest herbs, including some large-seeded species, such as *Viola riviniana*, are dispersed by ants (Kjellsson, 1985). The large seeds of the ubiquitous *Rubus fruticosus* are bird-dispersed.

Several species with wind-dispersed seeds were recorded in the seed rain but not in either the ground flora or seed bank, for example *Chamaenerion angustifolium*, *Lapsana communis* and *Hypochoeris radicata*. These are species which can colonise from rides and clearings.

Most of the species present in the seed rain were small-seeded species such as *Juncus effusus*, *Calluna vulgaris*, *Digitalis purpurea*, *Hypericum pulchrum*, *Betula spp*. and *Carex spp*. These species were generally present in the seed banks. At the sites studied, the species composition of the seed rain was more similar to that of the seed bank than the vegetation. In contrast, other studies which have recorded seed rain in forest communities (eg. Kellman, 1974) have found that the seed rain and vegetation have more species in common than the seed rain and seed bank.

Overall, seed inputs were low and no species was present at high densities. Seed inputs were particularly low at the abandoned coppice sites, both at Buckley and Blanchdown Woods. The felled area at Buckley Wood had a higher seed input than either the abandoned coppice or the larch plantation. This was mainly due to the open conditions, which promote flowering and seed production. The seed input for the cut coppice at Blanchdown Wood was low, *Agrostis capillaris* and *Juncus effusus* were the only species characteristic of open conditions recorded in this plot and not in either the Bradford Plan unit or the abandoned coppice plot. The seed inputs in the conifer stands at the Werrington Woods were not noticeably different for plantations of different ages or species.

The reliability of the data is affected by the small surface area used in each sample plot to monitor the seed rain (0.242 m^2) and the relatively short period of seed trapping. Some of the trapped seed may have been lost or germinated and died before the trays were collected and some seed may have failed to germinate in the greenhouse. Estimated seed inputs (seeds.m^{-2}) were much lower than estimated seed densities in the soils (Table 6.1.). The results indicate that seed inputs are higher after felling and very low beneath old canopies. This has also been shown by Kellman (1974) in a study which compared seed inputs in an undisturbed forest community in British Columbia, Canada, with those in an adjacent secondary community which had developed after clear-cutting. He found that seed inputs were much higher in the latter. Over a three year period, the amounts of seed of the commoner species trapped in any one year were less than the amounts present in the soil, suggesting that seeds accumulate in the soil over a period of years.

5.5. RIDE SURVEY

Species present in the ground flora and seed bank in the ride transect at the Tavistock Woodlands Estate are shown in Tables 5.12a. and 5.12b. respectively. Estimated viable seed densities for the six most common species and for the entire seed bank are shown in Figure 5.5.

At this site, the seed bank density was higher in the ride, particularly at the ride edges, than beneath the canopies. The seeds of *Juncus effusus* and *Agrostis spp.* were particularly abundant in the ride and at the ride edges. Seeds of *Holcus lanatus* also occurred mainly in the ride but only in low numbers. These three species are characteristic of woodland rides and clearings. The ground-flora survey showed that *Holcus lanatus*, *Agrostis capillaris* and *A. stolonifera* were present only in the ride and at the ride edges. *Juncus effusus* was not recorded in the ground flora survey, but must have been present at the site previously. Seeds of *Rubus fruticosus*, *Calluna vulgaris* and *Ulex gallii* occurred at lower densities in the ride than beneath the canopies and these species were also absent from the ride ground flora.

Species present in the ground flora and seed bank in the two ride transects at the Werrington Park Estate are shown in Tables 5.13a., 5.13b., 5.14a. and 5.14b. Estimated viable seed densities for the five or six most common species and for the entire seed bank are shown in Figures 5.6. and 5.7.

In the first transect, the most abundant species in the seed bank was *Juncus effusus*, although this species was not recorded in the ground flora. The high seed densities

Table 5.12a. Ride Transect: Species in the ground flora. Tavistock Woodlands Estate. 1-8 represent sampling points.

Species	Canopy			Ride			Canopy	
	1	2	3	4	5	6	7	8
Agrostis capillaris	-	-	-	+	+	-	-	-
Agrostis stolonifera	-	-	-	+	+	-	-	-
Dactylis glomerata	-	-	-	-	+	+	-	-
Hedera helix	+	+	-	-	-	-	+	+
Holcus lanatus	-	-	-	+	+	+	-	-
Holcus mollis	-	-	-	+	+	-	-	-
Lonicera periclymenum	-	-	+	-	-	+	-	-
Molinia caerulea	-	-	-	-	+	-	-	-
Potentilla erecta	-	-	-	+	+	-	-	-
Pteridium aquilinum	+	+	+	-	-	+	-	-
Ranunculus repens	-	-	-	+	-	-	-	-
Rubus fruticosus	+	+	+	-	+	+	-	+
Succisa pratensis	-	-	-	+	+	-	-	-
Vaccinium myrtillus	-	-	-	-	-	-	-	+
Total no. of species	3	3	3	7	9	5	1	3

Table 5.12b. Ride Transect: Species in the seed bank. Tavistock Woodlands Estate. 1-8 represent sampling points.

Species	Canopy			Ride			Canopy	
	1	2	3	4	5	6	7	8
Agrostis spp.	6	12	19	84	108	326	15	2
Calluna vulgaris	2	5	12	-	1	11	35	24
Carex pilulifera	-	-	-	-	-	11	-	-
Digitalis purpurea	-	-	-	-	1	-	-	-
Holcus lanatus	3	-	-	20	6	21	-	1
Hypericum pulchrum	-	-	-	1	-	-	-	-
Juncus effusus	-	-	284	82	152	72	13	5
Luzula pilosa	1	-	-	-	-	-	-	-
Poa spp.	3	-	-	-	2	1	-	1
Potentilla erecta	-	-	-	-	3	-	-	-
Rubus fruticosus	7	10	20	2	2	17	8	16
Ulex gallii	2	1	14	-	-	14	37	35
Total no. of seeds	24	28	349	189	275	473	108	84
Total no. of species	7	4	5	5	8	8	5	7

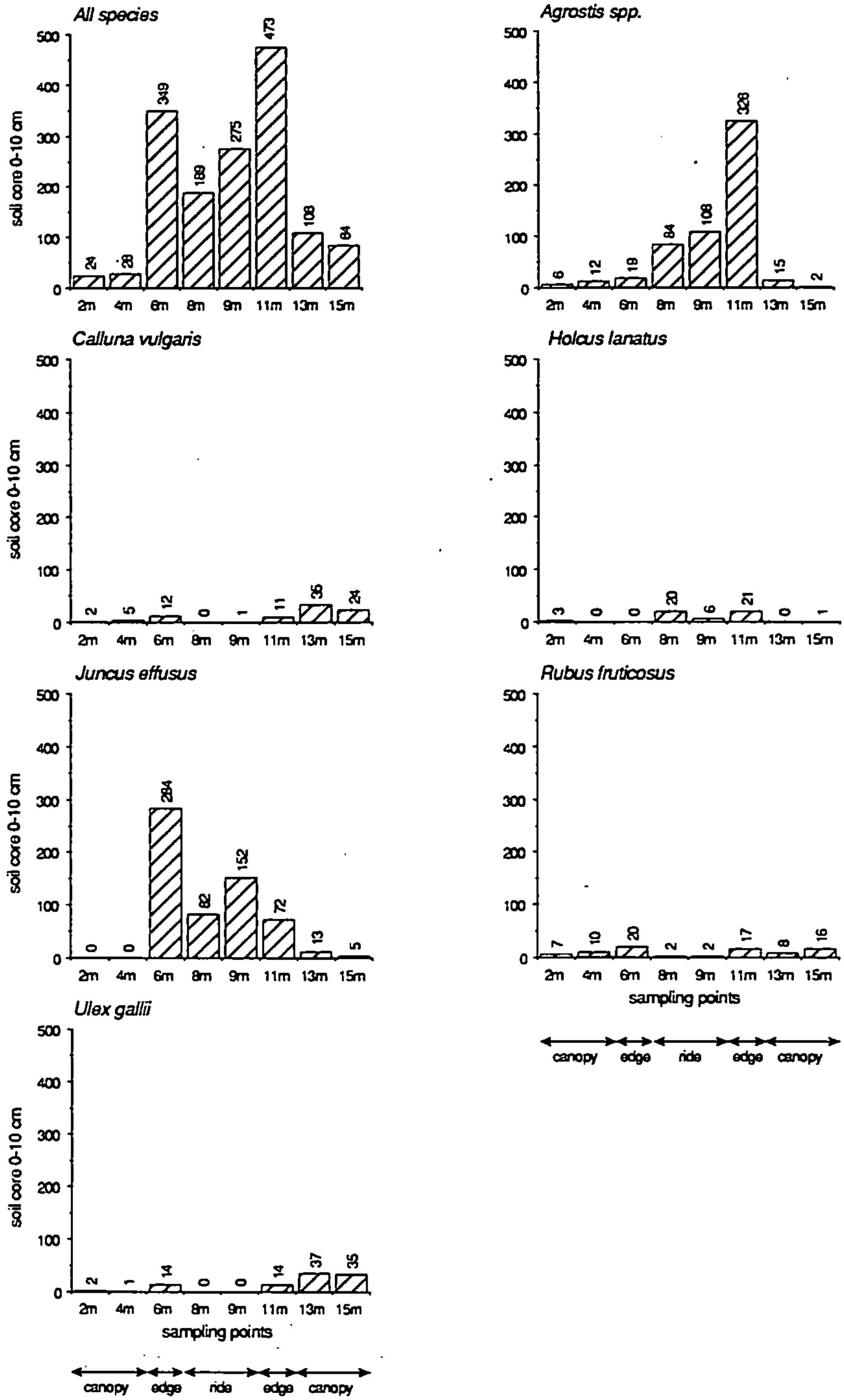


Figure 5.5. Ride Survey : Tavistock Woodlands Estate. Estimated viable seed densities (seeds.m^{-2}) for the entire seed bank & for the six most common species

Table 5.13a. Ride Transect: Species in the ground flora. Werrington Park Estate: Transect 1. 1-8 represent sampling points.

Species	Canopy			Ride			Canopy	
	1	2	3	4	5	6	7	8
Cardamine flexuosa	-	-	-	-	+	-	-	-
Circaea lutetiana	-	-	-	-	+	-	-	-
Cirsium palustre	-	-	-	+	-	-	-	-
Digitalis purpurea	-	-	-	+	-	-	-	-
Dryopteris affinis	-	-	+	+	+	+	-	-
Dryopteris dilatata	-	-	-	+	+	+	-	+
Dryopteris filix-mas	-	-	-	-	-	-	+	-
Epilobium spp.	-	-	-	+	-	-	-	-
Geranium robertianum	-	-	-	-	+	-	-	-
Oxalis acetosella	-	-	-	+	+	-	-	-
Lonicera periclymenum	-	-	+	+	+	+	-	-
Ranunculus repens	-	-	-	+	+	+	-	-
Rubus fruticosus	-	-	+	+	+	+	-	-
Total no. of species	0	0	3	9	9	5	1	1

Table 5.13b. Ride Transect: Species in the seed bank. Werrington Park Estate: Transect 1. 1-8 represent sampling points.

Species	Canopy			Ride			Canopy	
	1	2	3	4	5	6	7	8
Agrostis spp.	12	12	-	4	-	3	1	14
Betula spp.	3	24	19	13	5	8	8	47
Cardamine flexuosa	-	1	-	-	1	2	5	-
Carex pilulifera	1	2	-	-	-	-	-	-
Cerastium fontanum	-	-	-	-	-	1	-	-
Cirsium palustre	-	-	-	1	-	-	-	-
Cirsium vulgare	1	-	-	-	-	-	-	-
Digitalis purpurea	122	16	4	44	37	12	4	42
Geranium robertianum	-	1	2	3	3	-	1	2
Glechoma hederacea	-	-	-	-	1	-	1	-
Holcus lanatus	4	2	-	-	-	-	-	1
Hypericum pulchrum	1	20	8	2	-	3	1	-
Juncus effusus	327	387	325	285	189	111	128	47
Lotus corniculatus	-	2	-	6	-	-	-	-
Lysimachia nummularia	-	-	1	-	-	-	4	-
Ranunculus repens	12	13	69	6	34	13	85	5
Rubus fruticosus	10	6	57	46	18	12	3	25
Rumex acetosella	22	1	1	-	-	-	7	1
Scrophularia auriculata	1	-	-	-	-	-	-	-
Silene dioica	18	9	1	-	2	6	-	10
Stachys sylvatica	4	1	-	-	-	-	-	1
Stellaria media	-	-	-	-	-	8	-	-
Ulex gallii	3	24	12	5	-	-	-	-
Veronica chamaedrys	1	1	-	-	1	-	4	-
Veronica serpyllifolia	-	-	1	-	-	-	-	-
Viola riviniana	-	-	1	-	-	-	-	-
Total no. of seeds	542	522	501	415	291	179	252	195
Total no. of species	16	17	13	11	10	11	13	11

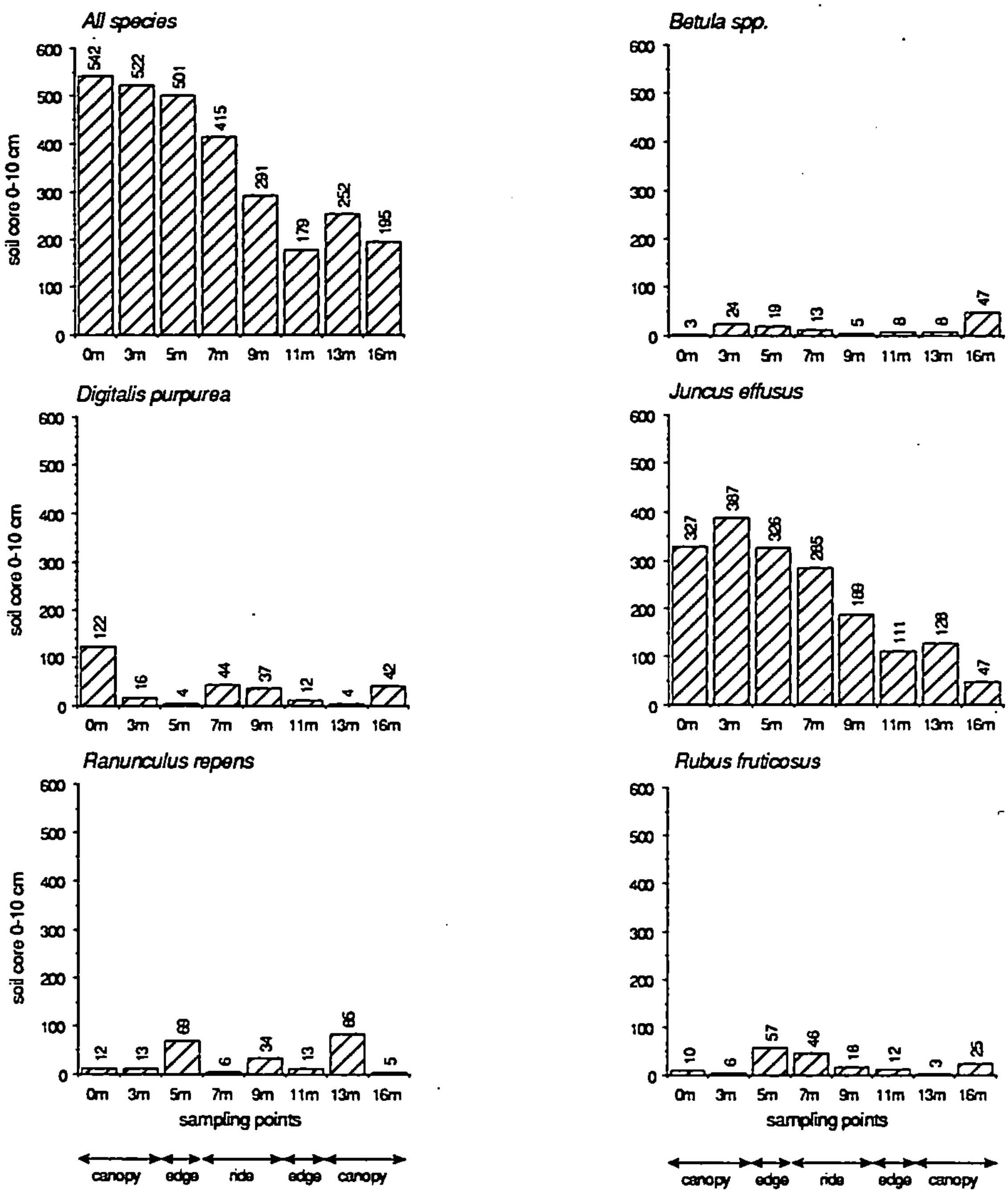


Figure 5.6. Ride Survey : Werrington Park Estate, Transect 1. Estimated viable seed densities (seeds.m^{-2}) for the entire seed bank & for the five most common species

Table 5.14a. Ride Transect: Species in the ground flora. Werrington Park Estate: Transect 2. 1-8 represent sampling points.

Species	Canopy		Ride				Canopy	
	1	2	3	4	5	6	7	8
Agrostis capillaris	-	-	-	+	+	-	-	-
Agrostis stolonifera	-	-	+	+	+	+	-	-
Athyrium filix-femina	-	-	-	-	-	+	-	-
Blechnum spicant	+	-	-	-	-	-	-	-
Cardamine flexuosa	-	-	-	+	-	-	-	-
Carex demissa	-	-	-	+	+	-	-	-
Dryopteris dilatata	+	+	+	+	-	-	+	+
Galium palustre	-	-	-	-	+	+	-	-
Hedera helix	+	+	+	+	-	+	+	+
Holcus lanatus	-	+	+	+	+	+	-	-
Holcus mollis	-	-	+	+	+	+	-	-
Hypericum pulchrum	-	-	-	-	-	+	-	-
Juncus bufonius	-	-	-	-	+	-	-	-
Juncus effusus	-	-	-	-	+	+	-	-
Lonicera periclymenum	+	+	+	+	-	-	-	-
Lysimachia nummularia	-	-	+	+	+	-	-	-
Oxalis acetosella	+	-	+	-	-	+	-	+
Pteridium aquilinum	+	+	+	+	-	+	+	+
Ranunculus flammula	-	-	-	-	+	-	-	-
Rubus fruticosus	+	+	+	-	-	+	+	+
Silene dioica	-	-	+	-	-	+	-	-
Teucrium scorodonia	-	-	+	-	-	-	+	-
Veronica montana	-	-	+	+	-	-	-	-
Viola riviniana	-	-	+	-	-	-	-	-
Total no. of species	7	6	14	12	10	12	5	5

Table 5.14b. Ride Transect: Species in the seed bank. Werrington Park Estate: Transect 2. 1-8 represent sampling points.

Species	Canopy		Ride				Canopy	
	1	2	3	4	5	6	7	8
Agrostis spp.	6	15	22	24	10	16	19	7
Ajuga reptans	2	-	-	-	-	-	6	1
Betula spp.	35	18	16	21	7	3	10	7
Calluna vulgaris	-	1	-	-	-	-	-	-
Cardamine flexuosa	-	-	2	2	1	4	-	-
Carex spp.	6	3	2	18	1	4	2	1
Digitalis purpurea	1	29	7	13	3	4	3	4
Galium saxatile	2	-	-	-	-	-	-	-
Holcus lanatus	-	-	21	5	5	13	10	3
Hypericum pulchrum	-	2	-	-	-	2	-	3
Juncus spp.	151	49	106	109	48	124	133	54
Luzula pilosa	-	-	-	1	-	1	-	-
Poa spp.	2	-	15	1	4	1	2	-
Potentilla erecta	1	-	-	-	-	-	-	-
Ranunculus flammula	-	-	-	-	-	-	-	1
Ranunculus repens	-	-	-	1	-	-	-	1
Rubus fruticosus	10	3	11	-	-	11	10	4
Rumex obtusifolius	1	2	-	-	-	-	-	-
Silene dioica	-	-	-	-	-	-	1	-
Stellaria media	-	-	-	2	1	-	-	-
Teucrium scorodonia	-	-	-	-	-	-	2	3
Ulex gallii	-	1	-	-	-	-	2	5
Veronica montana	-	1	1	1	-	-	-	-
Viola riviniana	1	-	-	-	-	-	-	1
Total no. of seeds	218	124	203	198	80	183	200	95
Total no. of species	12	11	10	12	9	11	12	14

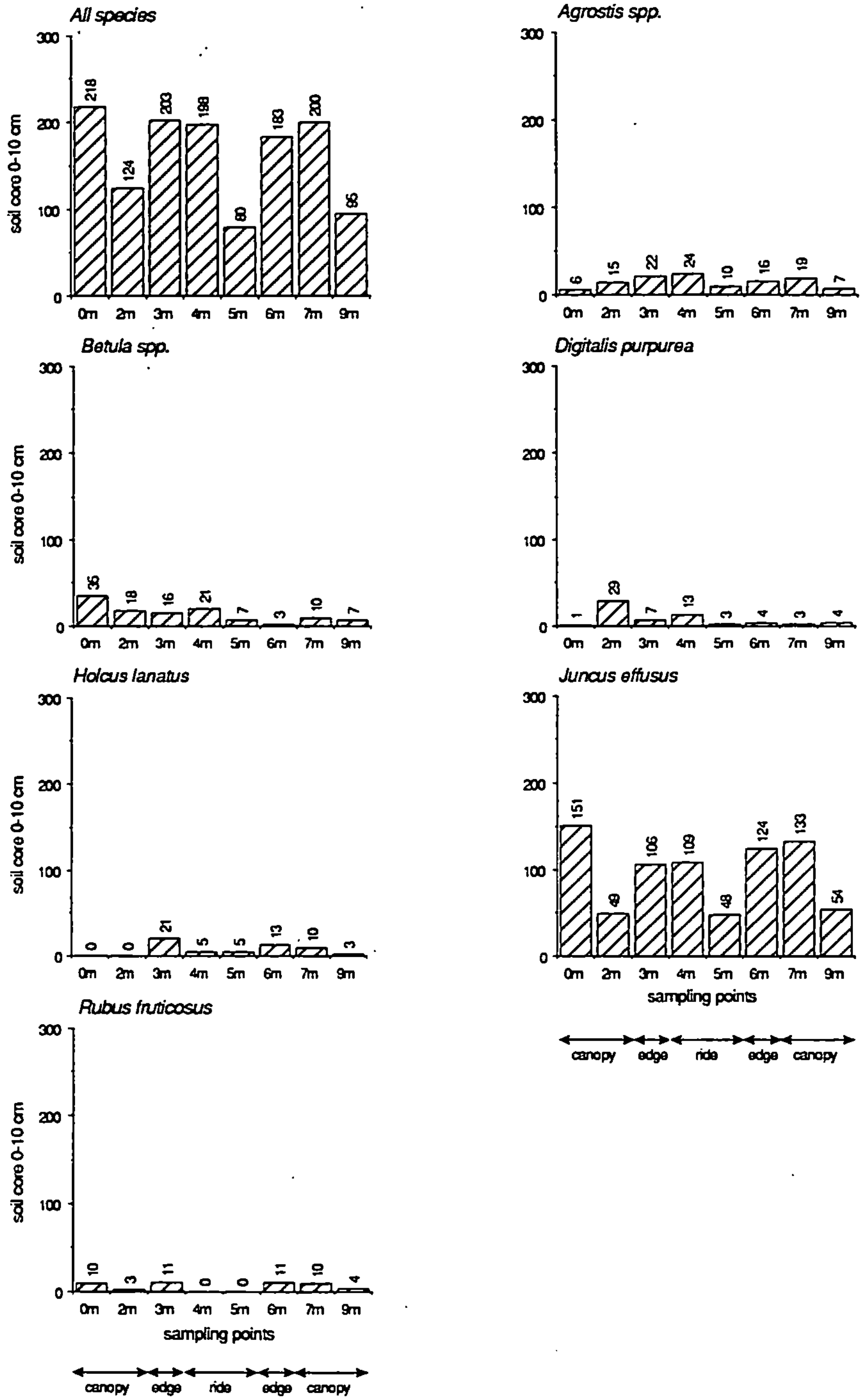


Figure 5.7. Ride Survey : Werrington Park Estate, Transect 2. Estimated viable seed densities (seeds.m^{-2}) for the entire seed bank & for the six most common species

suggest that the species must have been present in the ground flora previously. The seed densities of this species at this site were not higher in the ride than beneath the canopies. The seeds of *Ranunculus repens* and *Rubus fruticosus* were more abundant in the ride and ride edge than beneath the canopies, and these two species were only recorded in the ground flora of the ride and ride edge. The presence of *Rubus fruticosus* in the ground flora of the ride is an indication that this ride is not frequently disturbed. *Digitalis purpurea* and *Betula spp.* were also common in the seed banks. The seeds of these species were not more abundant in the ride than beneath the canopies, although *Digitalis purpurea* was present only in the ride ground flora. No grasses were recorded in the ground flora of the ride and seeds of *Holcus lanatus* and *Agrostis spp.* were only recorded at very low densities in the soil.

In the second transect there were fewer seeds in the soil, but again *Juncus effusus* was the predominant species in the seed bank. At this site the species was present in the ground flora of the ride but not beneath the canopies; however seed densities were not higher in the ride than beneath the canopies. *Rubus fruticosus* was absent from the ground flora of the ride and from the seed bank, but present in both the ground flora and seed bank of the ride edge and beneath the canopies. A number of grasses, including *Holcus lanatus*, *H. mollis*, *Agrostis stolonifera* and *A. capillaris* were present in the ground flora of the ride and ride edge. Seeds of *Agrostis spp.* and *Holcus lanatus* were more abundant in the ride and ride edge than beneath the canopies, but were only present at low densities. No seeds of *Holcus mollis* were recorded, but this species was much less abundant in the ground flora than *Holcus lanatus*. As in the first transect at this site, *Betula spp.* and *Digitalis purpurea* occurred frequently in the seed banks and were not especially abundant in the ride.

Species present in the ground flora and seed bank in the ride transect at the Lindridge Estate are shown in Tables 5.15a. and 5.15b. respectively. Estimated viable seed densities for the four most common species and for the entire seed bank are shown in Figure 5.8. The seed bank density was slightly higher in the ride than beneath the canopies at this site. One species, *Hypericum perforatum* was predominant in the seed bank. A few seedlings of *H. montanum* and *H. hirsutum* were also recorded in the germination trials but these were not counted separately. Seeds of *Hypericum perforatum* were abundant across the transect, despite the absence of the species from the ground flora. Another species which occurred frequently in the seed bank was *Urtica dioica*; this species was recorded only in the ride ground flora. A large number of species which were growing only in the ride and ride edge were present only in the ride seed bank but seeds generally occurred at low densities, for example, *Viola riviniana*, *Glechoma hederacea*, *Ajuga reptans*, *Lapsana communis*, *Euphorbia amygdaloides*, and grasses such as *Brachypodium sylvaticum*, *Festuca gigantea* and *Poa annua*. The seeds of two species, *Centaurium erythraea* and *Ranunculus repens*, also present only in the ride ground flora, occurred at slightly higher densities in the ride seed bank. *Rubus fruticosus* was growing only in the ride and along the ride edge at this site, but few seeds were found in the seed bank.

Table 5.16. shows the number of species in the seed bank and ground flora in the four transects. At all sites, there are fewer species in the ground flora beneath the canopies than in the rides. The ride at the Tavistock Woodlands Estate is the least diverse, that at the Lindridge Estate the most and the two at the Werrington Park Estate intermediate. The number of species in the seed bank is more variable, there are not

Table 5.15a. Ride Transect: Species in the ground flora. Lindridge Estate. 1-10 represent sampling points.

Species	Canopy				Ride				Canopy	
	1	2	3	4	5	6	7	8	9	10
Ajuga reptans	-	-	-	-	+	-	-	-	-	-
Brachypodium sylvaticum	-	-	-	+	+	+	-	-	-	-
Cardamine hirsuta	-	-	-	-	-	-	-	-	-	-
Carex sylvatica	-	-	-	-	-	+	-	-	-	-
Centaurium erythraea	-	-	-	-	-	+	-	-	-	-
Crataegus monogyna	-	-	-	-	-	+	-	-	-	-
Dryopteris affinis	-	-	-	-	-	-	-	-	+	-
Dryopteris filix-mas	-	-	-	-	-	-	+	-	-	-
Epilobium spp.	-	-	-	-	+	+	-	-	-	-
Euphorbia amygdaloides	-	-	-	+	+	-	-	-	-	-
Festuca gigantea	-	-	-	+	+	+	-	-	-	-
Geranium robertianum	-	-	-	-	-	+	-	-	-	-
Glechoma hederacea	-	-	-	+	+	+	-	-	-	-
Hedera helix	-	+	+	+	+	+	+	+	+	+
Lapsana communis	-	-	-	+	+	+	-	-	-	-
Mercurialis perennis	-	-	+	+	-	+	+	+	+	+
Phyllitis scolopendrium	+	-	+	-	-	-	+	+	+	+
Pteridium aquilinum	-	-	-	+	-	-	-	-	-	-
Poa annua	-	-	-	-	+	+	-	-	-	-
Potentilla sterilis	-	-	-	+	-	-	-	-	-	-
Prunella vulgaris	-	-	-	+	+	+	-	-	-	-
Ranunculus repens	-	-	-	+	+	+	+	-	-	-
Rubus fruticosus	-	-	-	+	+	+	+	-	-	-
Rumex sanguineus	-	-	-	-	-	+	-	-	-	-
Urtica dioica	-	-	+	+	-	-	+	+	-	-
Veronica chamaedrys	-	-	-	+	+	+	-	-	-	-
Viola riviniana	-	-	-	+	+	+	-	-	-	-
Total no. of species	1	1	4	15	14	18	7	4	4	3

Table 5.15b. Ride Transect: Species in the seed bank. Lindridge Estate. 1-10 represent sampling points.

Species	Canopy			Ride				Canopy		
	1	2	3	4	5	6	7	8	9	10
Agrostis spp.	-	1	-	-	5	-	-	-	-	-
Ajuga reptans	-	-	-	2	2	1	-	-	-	-
Betula pendula	1	2	1	-	-	-	1	4	-	4
Buddleja davidii	-	1	-	-	-	-	-	-	-	-
Brachypodium sylvaticum	-	-	-	-	-	1	-	-	-	-
Cardamine hirsuta	-	-	5	2	3	2	-	-	-	-
Carex sylvatica	-	-	-	-	-	1	-	-	-	-
Centaurium erythraea	1	-	9	12	51	12	-	-	-	-
Cerastium fontanum	-	-	-	-	3	5	-	-	-	-
Cirsium arvense	1	-	-	-	-	1	2	2	-	-
Cirsium vulgare	-	1	-	1	-	-	-	2	1	-
Clematis vitalba	-	-	1	-	-	-	1	2	-	1
Eupatorium cannabinum	-	1	1	-	-	-	-	-	-	2
Euphorbia amygdaloides	-	-	1	-	-	-	-	-	-	-
Glechoma hederacea	-	-	-	-	-	3	-	3	-	2
Hypericum spp.	54	49	58	68	26	69	42	45	110	43
Lapsana communis	-	-	-	1	1	-	1	-	-	-
Poa annua	-	-	-	6	29	14	-	-	-	-
Ranunculus repens	17	11	4	-	33	41	10	28	-	2
Rubus fruticosus	1	2	2	8	-	1	1	3	-	-
Rumex acetosa	9	1	-	-	-	-	-	-	2	1
Silene alba	-	-	-	-	-	1	-	-	-	-
Torilis japonica	-	-	-	2	1	-	-	-	1	-
Urtica dioica	6	26	17	11	7	6	8	5	-	5
Verbascum thapsus	2	5	2	2	2	7	-	5	-	-
Veronica chamaedrys	-	-	1	-	-	2	-	-	-	-
Veronica montana	-	1	-	-	-	10	-	-	-	-
Veronica officinalis	-	-	-	-	1	-	-	-	1	4
Viola riviniana	-	-	-	4	1	-	-	-	-	-
Total no. of seeds	92	101	102	119	165	177	66	99	115	64
Total no. of species	9	12	12	12	14	17	8	10	5	9

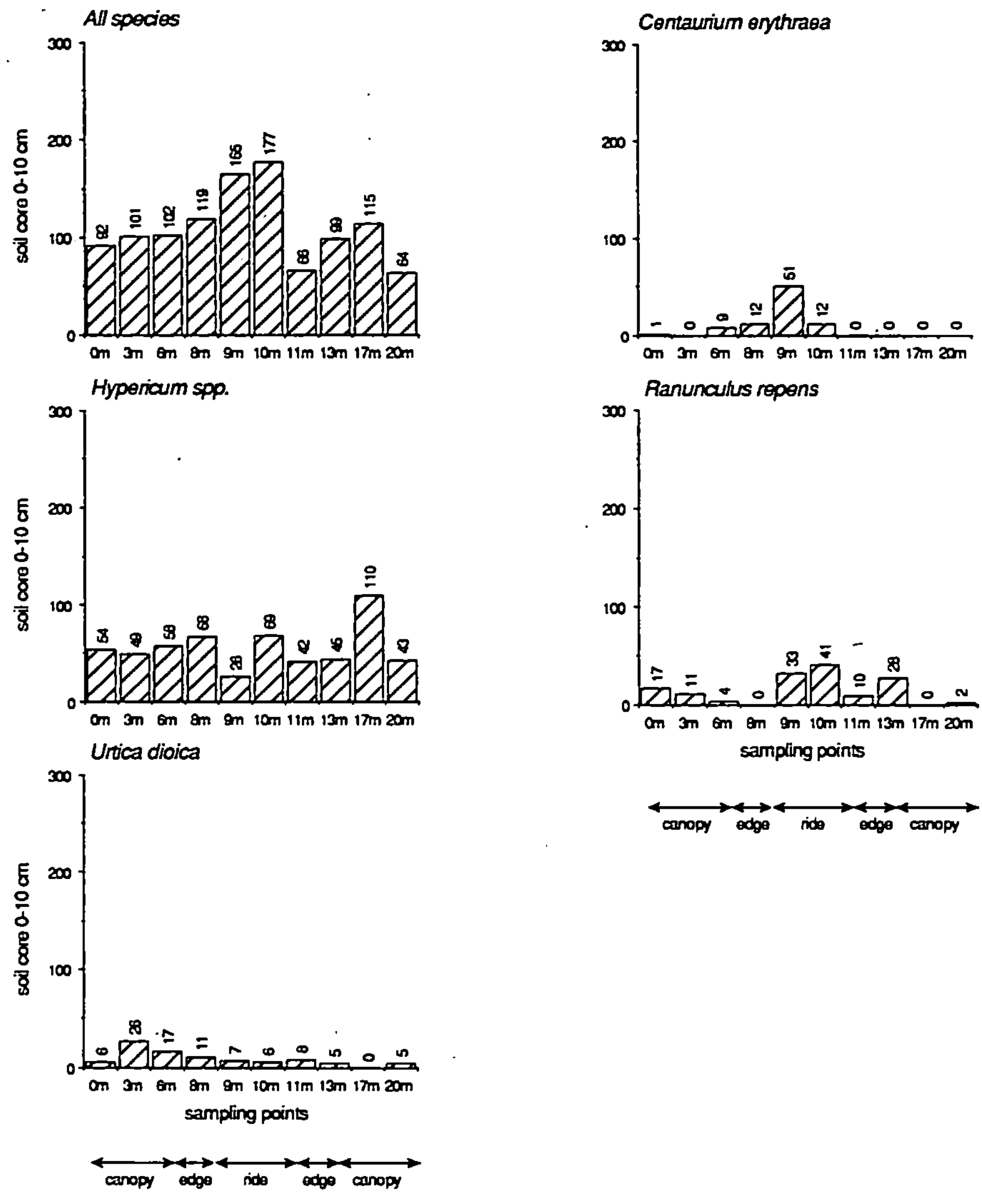


Figure 5.8. Ride Survey : Buckley Wood, Lindridge Estate. Estimated viable seed densities (seeds.m^{-2}) for the entire seed bank & for the four most common species

Table 5.16. Ride Transects: Number of species in the seed bank and ground flora.

Tavistock Woodlands Estate

No. of species	Canopy			Ride			Canopy	
in seed bank	7	4	5	5	8	8	5	7
in ground flora	3	3	3	7	9	5	1	3

Werrington Woods (Transect 1)

No. of species	Canopy			Ride			Canopy	
in seed bank	16	17	13	11	10	11	13	11
in ground flora	0	0	3	9	9	5	1	1

Werrington Woods (Transect 2)

No. of species	Canopy			Ride			Canopy	
in seed bank	12	11	10	12	9	11	12	14
in ground flora	7	6	14	12	10	12	5	5

Buckley Wood

No. of species	Canopy				Ride				Canopy	
in seed bank	9	12	12	12	14	17	8	10	5	9
in ground flora	1	1	4	15	14	18	7	5	4	3

necessarily more species present in the seed bank of the ride than in that beneath the canopies.

For some species a strong association occurs between presence in the ground flora and seed bank. This applies to the grasses and many of the other species found growing only in rides and is illustrated well by the Buckley Wood data.

The presence of seeds of *Rubus fruticosus* did not always coincide with the presence of the species in the ground flora. This is probably because the seeds can survive for relatively long periods in the soil and are actively dispersed by birds. Species with wind dispersed seeds, for example, *Betula spp*., also show no association with rides.

A number of species which occur at high densities in the soil, such as *Juncus effusus*, *Hypericum spp*. and *Digitalis purpurea* are as abundant beneath the canopies as in the rides. The time since canopy closure is likely to influence the abundance of these species. Darby (1987) showed that beneath the closed canopy of abandoned coppice, long-lived species such as *Juncus effusus* eventually became less abundant, but peaks of seed density coinciding with rides remained. The distribution of seeds of *Juncus effusus* in the ride transect at the Tavistock Woodlands Estate is similar to that observed by Darby (1987). It can be concluded that for some species, rides provide a reserve of seeds which may be important for the survival of these species if seed bank depletion beneath closed canopies takes place.

5.6. CONCLUSION

In this chapter, the results of the phase II seed bank sampling and ground flora surveys have been presented, together with the results of the seed rain and ride surveys. In chapter six, the results of both the phase I and phase II seed bank surveys are discussed and differences in germination from the phase I and phase II samples are examined.

CHAPTER SIX : WITHIN AND BETWEEN SITE COMPARISONS

6.1. INTRODUCTION

In this chapter, for each of the five sites studied, within and between site differences in seed bank densities and species compositions are discussed. The results from both phases of sampling are compared with those of other studies. This chapter also considers the reasons for excluding some species, recorded in the germination tests, from the results of the surveys. Finally, differences in germination from the phase I and phase II soil samples are examined.

6.2. SEED BANK DENSITIES AND SPECIES COMPOSITIONS

Estimated viable seed densities in the 0-5 cm soil layer for the phase II samples are shown in Figure 6.1a. (acid sites) and 6.1b. (basic sites). There is apparently no simple relationship between seed densities and either acid or basic soils or coniferous or broadleaved canopies. Seed densities are lower at Buckley Wood, in both the coniferous and broadleaved stands, on basic soils, than in the conifer stands at Werrington and Longleat Woods, on acid soils. However, low seed densities in the oak and birch stands at Yarner Wood, on acid soils, and high seed densities in the Longleat oak stands, on basic soils, indicate that high seed densities are not necessarily associated with acid soils. Within and between site differences in seed densities appear to be attributable to a large extent to the presence or absence of two species, *Calluna vulgaris* and *Juncus effusus*. These species produce large numbers of very small seeds which are long-lived in the soil. The presence of high seed

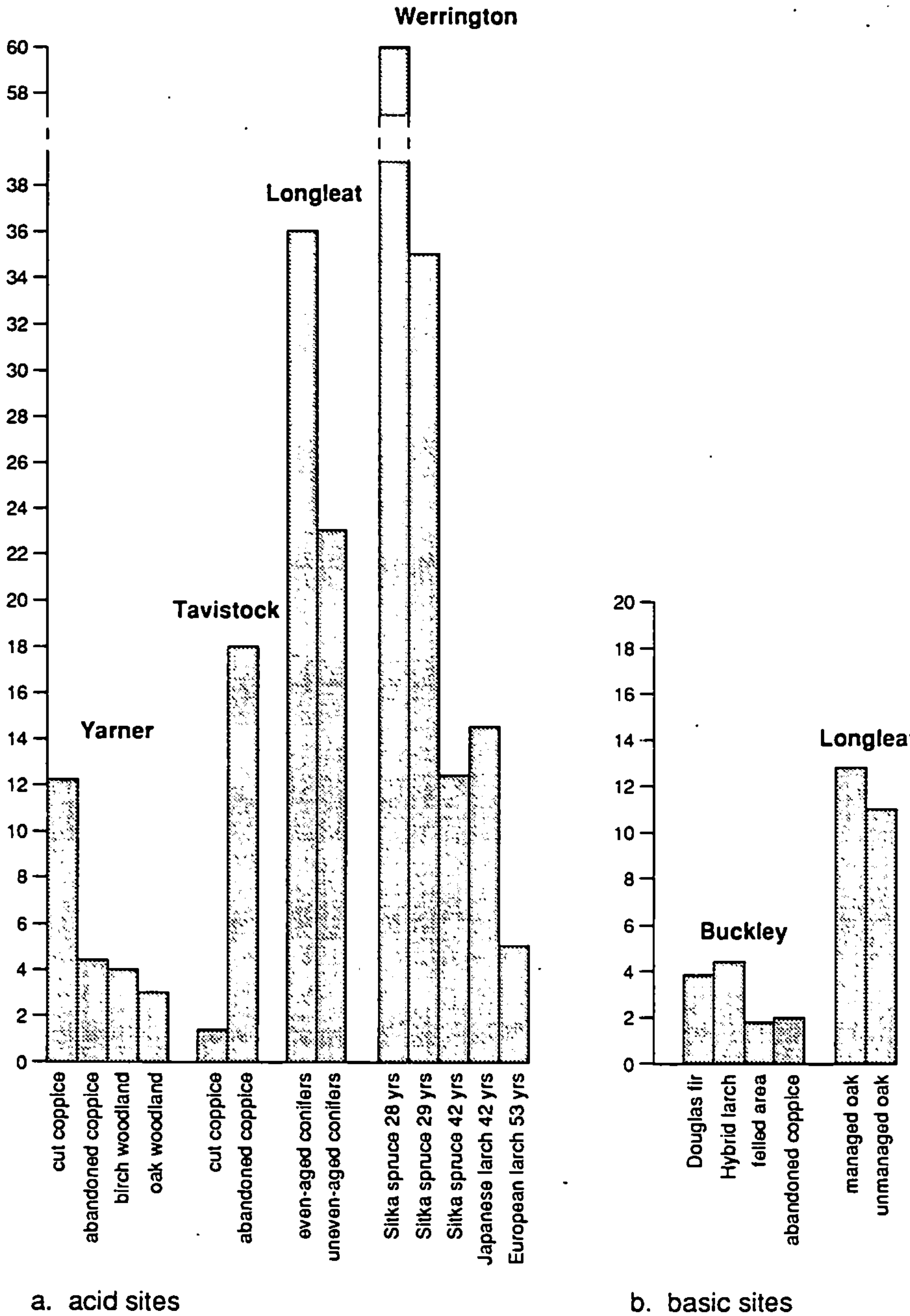


Figure 6.1 Estimated viable seed densities (seeds.m^{-2}) in the 0-5 cm soil layer for the Phase II samples

densities in the soils of *Calluna*-dominated upland vegetation has long been recognized (Chippindale & Milton, 1934). Champness & Morris (1948) found that the buried seed population of moorlands was greatly affected by the presence or absence of *Calluna* and *Juncus*. These two genera are associated with the moorland, heaths and bogs on which upland conifer plantations are often established. Both are common in lowland, damp and acid woodlands such as the Longleat conifer stands, the Tavistock Woodlands and the Werrington conifer plantations. *Calluna* is also abundant on the infertile acid soils at Yarner Wood on the edge of Dartmoor, but absent from the more fertile basic soils at Buckley Wood and Blackdog Wood.

Seed densities at Yarner Wood were low in the abandoned coppice, birch and oak woodland, but were higher in the cut coppice. This was mainly due to higher numbers of *Calluna* seeds in the cut coppice. At Blanchdown Wood seed densities were higher in the abandoned coppice than in the cut coppice, again due to an abundance of *Calluna* seeds in the abandoned coppice.

At Blanchdown and Grenoven Woods, more seeds were present in the younger, most recently cleared Bradford Plan sub-units. The number of *Juncus* seeds present in the younger sub-units was greater than in the older sub-units but there were also higher numbers of seeds of other species which had become more abundant in the ground flora of the cleared sub-units. The decline in seed density with sub-unit age is shown in Figure 6.4a. For the phase II samples, apart from the low seed density found in the 15 year-old sub-unit, a straight line is obtained on a log-log plot, indicating an exponential decay curve.

In the conifer stands on the Longleat Estate, high seed densities were recorded, particularly in the even-aged stand. *Calluna* seeds were abundant in both the uneven- and even-aged stands and *Juncus* seeds in the even-aged stand. At the Werrington Park Estate, very high seed densities were found in the two youngest plantations. *Juncus* seeds were very abundant in the seed banks of these plantations. Seed densities were lower in the three older plantations; both *Calluna* and *Juncus* seeds were present in the seed banks, but not at very high densities. The oldest plantation had the lowest seed density. The decline in seed density with plantation age is shown in Figure 6.5a. For both the phase I and phase II samples, a straight line is obtained on a log-log plot, indicating exponential decline.

At Buckley Wood, where no *Calluna* or *Juncus* seeds were present, seed densities were much lower. In the oak stands at Blackdog Wood, *Juncus* was abundant and seed densities were higher.

The species recorded in the seed banks at the five sites are shown in Tables 6.1a. (acid sites) and 6.1b. (basic sites). These are combined data for the phase I (0-5 cm) and phase II (0-5, 5-10 and 10-15 cm) samples. Some species were present at both the acid and the basic sites, for example *Rubus fruticosus* and *Stachys sylvatica*. Others were present only at the acid sites, such as *Digitalis purpurea* and *Calluna vulgaris*, or the basic sites, such as *Moehringia trinervia* and *Glechoma hederacea*.

The numbers of species present in the seed banks and ground floras are shown in Figures 6.2a. and 6.3a. (acid sites) and 6.2b. and 6.3b. (basic sites). The number of species present in the ground flora is more variable than that in the seed bank because

Table 6.1a. Species in the seed banks of the four infertile (acid) sites (Phase I and Phase II samples).

Species	Yarner Wood				Tavistock Woodlands			Longleat Estate		Werrington Estate				
	a	b	c	d	a	b	c	a	b	a	b	c	d	e
Agrostis capillaris	-	-	-	-	+	+	+	+	+	-	+	-	-	+
Agrostis stolonifera	-	-	-	-	-	-	+	+	+	+	-	+	+	-
Betula spp.	+	+	+	+	+	+	+	-	+	+	+	+	+	+
Calluna vulgaris	+	+	+	+	+	+	+	+	+	+	-	+	+	+
Carex pilulifera	+	+	-	+	+	+	+	+	+	+	-	+	+	+
Carex demissa	-	-	-	-	-	-	-	+	-	-	-	-	-	-
Chamaenerion angustifolium	-	-	-	+	-	-	-	-	-	-	+	-	-	-
Cerastium fontanum	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Cirsium arvense	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Digitalis purpurea	-	-	-	-	-	-	+	+	+	+	+	+	+	+
Galium saxatile	-	-	-	-	-	-	-	-	+	+	+	+	+	+
Geranium robertianum	-	-	-	-	-	-	-	-	-	+	-	+	-	-
Gnaphalium uliginosum	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Heracleum sphondylium	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Holcus lanatus	-	-	-	-	-	-	-	+	+	+	+	-	-	-
Hyacinthoides non-scripta	-	-	-	-	-	-	-	-	-	+	+	-	-	+
Hypericum pulchrum	-	-	-	-	-	-	+	+	+	-	+	+	+	-
Hypochoeris radicata	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Juncus bufonius	-	-	-	-	-	-	-	-	-	+	-	+	-	-
Juncus effusus	+	+	+	+	-	-	+	+	+	+	+	+	+	+
Lapsana communis	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Lotus corniculatus	-	-	-	-	-	-	-	-	+	-	+	-	-	-
Luzula pilosa	-	-	+	-	-	-	+	-	+	+	-	-	+	-
Oxalis acetosella	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Poa annua	+	-	+	-	+	+	-	-	-	+	-	+	+	+
Poa trivialis	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Potentilla erecta	-	-	-	-	-	-	-	-	+	-	-	+	+	-
Rubus fruticosus	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Rumex acetosa	+	+	-	+	-	-	-	+	+	-	-	-	-	-
Rumex acetosella	-	-	-	-	-	-	-	-	-	-	+	-	-	+
Rumex obtusifolius	-	-	-	-	-	+	-	-	-	+	-	+	+	-
Scrophularia auriculata	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Silene dioica	-	-	-	-	-	-	-	-	-	+	+	+	+	+
Stachys sylvatica	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Stellaria media	-	-	-	-	-	-	-	-	-	+	+	-	+	-
Teucrium scorodonia	-	-	-	-	-	-	+	+	-	+	-	+	-	-
Ulex gallii	-	-	-	-	-	+	+	+	+	+	+	+	+	+
Urtica dioica	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Vaccinium myrtillus	+	+	-	+	-	+	-	-	-	-	-	-	-	-
Veronica chamaedrys	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Veronica montana	-	-	-	-	-	-	-	+	-	-	-	-	-	-
Veronica officinalis	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Total no. of species	8	7	6	8	6	9	14	14	17	22	20	19	16	13

Key to Canopy Types

Yarner Wood
a Cut coppice
b Abandoned coppice
c Birch woodland
d Oak woodland

Tavistock Woodlands Estate
a Cut coppice
b Abandoned coppice
c B-Plan units

Longleat Estate
a Even-aged conifers
b Uneven-aged conifers

Werrington Park Estate
a Sitka spruce 28 yrs
b Sitka spruce 29 yrs
c Sitka spruce 42 yrs
d Japanese larch 42 yrs
e European larch 53 yrs

Table 6.1b. Species in the seed banks of the two fertile (basic) sites (Phase I and Phase II samples).

Species	Buckley Wood				Longleat Estate	
	a	b	c	d	a	b
Antirrhinum majus	♦	-	-	-	-	-
Agrostis capillaris	-	-	-	-	♦	♦
Agrostis stolonifera	♦	-	♦	-	♦	♦
Ajuga reptans	-	-	♦	♦	♦	♦
Arctium minus	♦	-	-	-	-	-
Betula spp.	♦	♦	♦	♦	♦	♦
Brachypodium sylvaticum	-	-	-	-	-	♦
Buddleja davidii	♦	♦	♦	♦	-	-
Cardamine flexuosa	-	-	-	-	♦	♦
Cardamine hirsuta	♦	♦	♦	-	-	-
Carex flacca	♦	♦	-	-	-	-
Carex pendula	-	-	-	-	♦	-
Carex remota	-	-	-	-	♦	-
Carex strigosa	-	-	-	-	-	♦
Carex sylvatica	-	-	-	-	♦	-
Chamaenerion angustifolium	♦	♦	♦	-	-	♦
Centaurium erythraea	♦	♦	♦	♦	-	-
Cerastium fontanum	-	-	♦	-	-	♦
Cirsium arvense	♦	♦	♦	♦	♦	-
Cirsium palustre	-	-	-	-	♦	-
Cirsium vulgare	♦	♦	♦	-	♦	-
Clematis vitalba	-	♦	♦	♦	-	-
Crataegus monogyna	-	♦	-	♦	-	-
Deschampsia caespitosa	-	-	-	-	♦	-
Eupatorium cannabinum	♦	♦	♦	-	-	-
Euphorbia amygdaloides	♦	♦	♦	♦	-	-
Fragaria vesca	-	-	-	-	♦	♦
Fraxinus excelsior	♦	-	-	♦	-	-
Galium aparine	-	-	-	-	♦	-
Geranium robertianum	-	-	-	-	♦	♦
Geum urbanum	♦	♦	-	-	-	♦
Glechoma hederacea	-	-	-	-	♦	♦
Holcus lanatus	♦	-	-	-	♦	-
Hypericum hirsutum	-	-	♦	-	-	-
Hypericum montanum	♦	♦	♦	♦	♦	♦
Hypericum perforatum	♦	♦	♦	♦	♦	♦
Hypericum tetrapterum	-	♦	-	-	-	-
Hypochoeris radicata	♦	-	-	♦	-	-
Iris foetidissima	♦	♦	♦	-	-	-
Juncus effusus	-	-	-	-	♦	♦
Lapsana communis	-	♦	♦	-	-	-
Luzula spp.	♦	-	-	-	♦	-
Lysimachia nemorum	-	-	-	-	-	♦
Moehringia trinervia	♦	♦	♦	-	♦	-
Myosotis arvensis	-	-	♦	-	-	-
Poa annua	♦	♦	♦	♦	-	-
Poa trivialis	♦	♦	♦	♦	♦	♦
Potentilla sterilis	♦	-	♦	♦	♦	♦
Primula vulgaris	♦	♦	♦	♦	-	♦
Ranunculus repens	♦	-	♦	♦	-	-
Rubus fruticosus	♦	♦	♦	♦	♦	♦
Rumex acetosa	♦	♦	♦	♦	-	♦
Sambucus nigra	-	♦	♦	♦	-	-
Scrophularia auriculata	-	-	-	-	♦	♦
Scrophularia nodosa	♦	♦	-	-	-	-
Senecio jacobaea	♦	-	♦	-	-	-
Senecio sylvaticus	-	-	♦	♦	-	-
Silene alba	-	♦	♦	-	-	-
Stachys sylvatica	-	♦	♦	-	-	-
Stellaria media	♦	-	-	-	-	-
Urtica dioica	♦	♦	♦	♦	-	-
Verbascum thapsus	♦	♦	-	♦	-	-
Veronica chamaedrys	♦	♦	♦	♦	♦	-
Veronica montana	♦	-	♦	-	♦	♦
Veronica officinalis	♦	-	-	♦	-	-
Veronica persica	♦	-	♦	-	-	-
Viola riviniana	♦	♦	-	-	♦	-
Total no. of species	39	32	36	25	29	24

Key to Canopy Types

Buckley Wood	Longleat Estate
a Douglas fir	a Cut coppice
b Hybrid larch	b Abandoned coppice
c Felled area	
d Abandoned coppice	

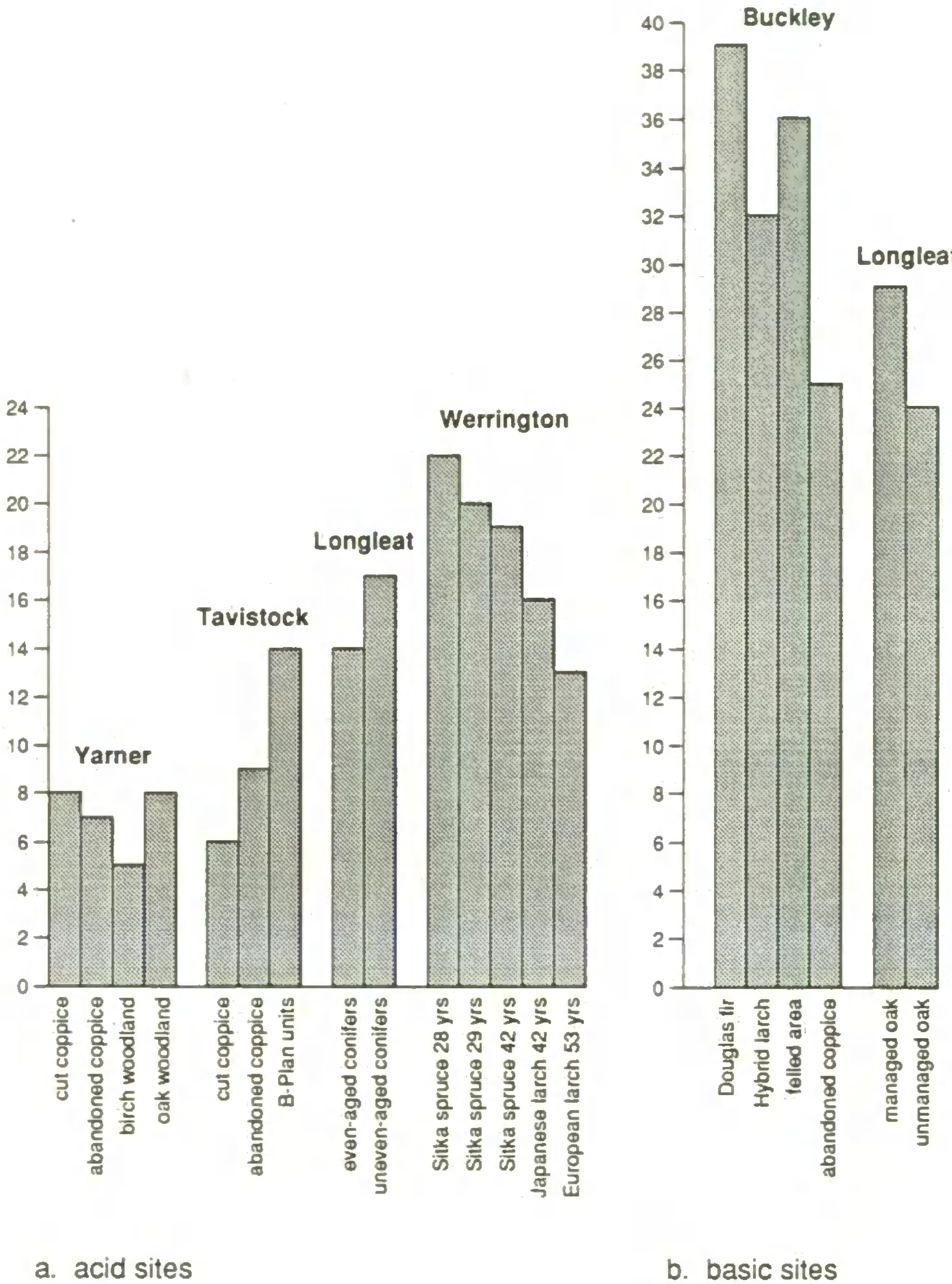


Figure 6.2 Number of species present in the seed bank

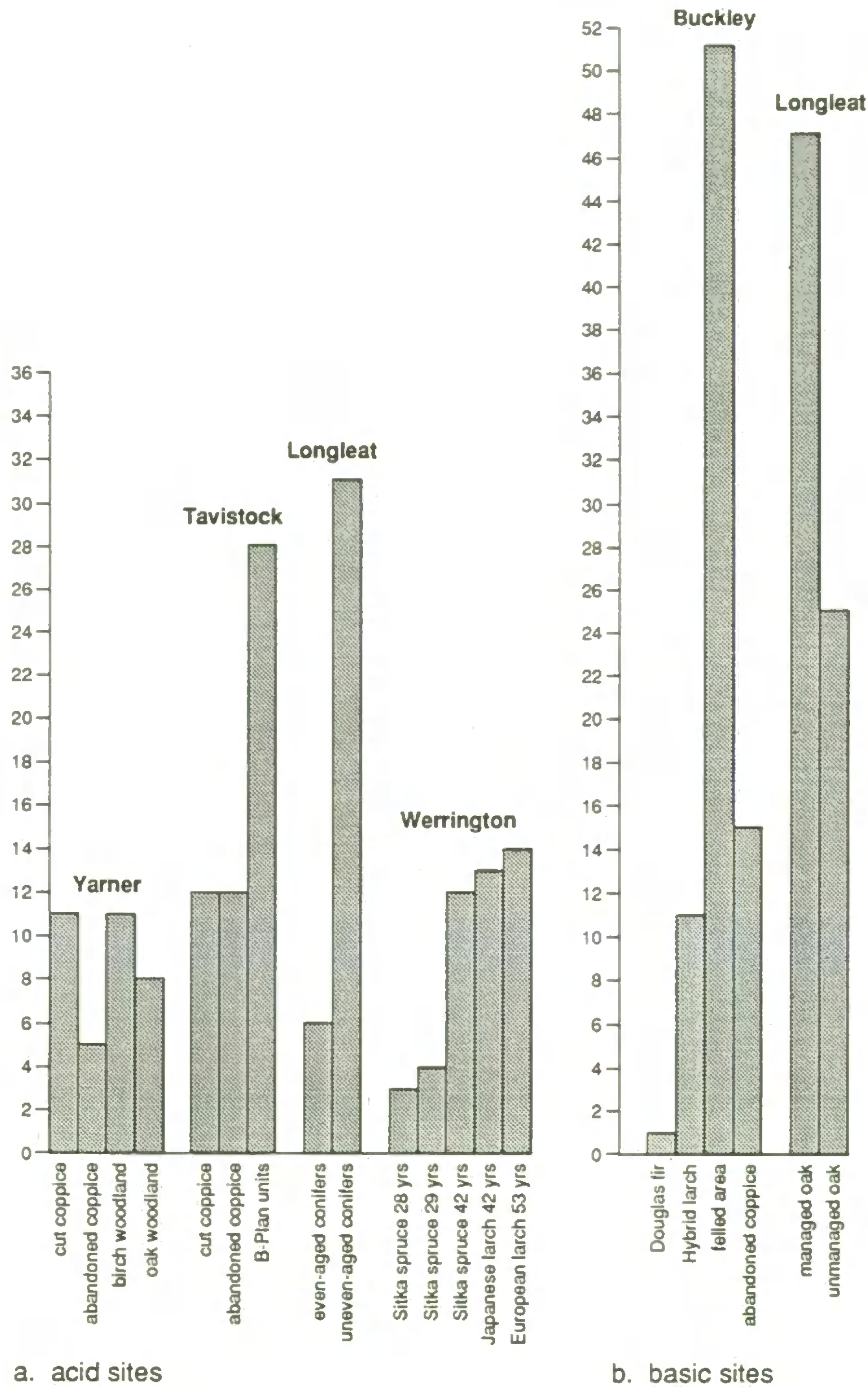


Figure 6.3 Number of species present in the ground flora

the effects of different management practices affect the ground flora more quickly than the seed banks. There are generally more species present at the basic sites than at the acid sites, particularly in the seed banks. A similar trend, ie. an increase in the number of species present with increasing soil fertility, was found by Staaf et al. (1987) for Swedish beechwoods.

At the acid sites, the alternative forestry management systems (B-Plan and uneven-aged conifers) are associated with an increased number of species in both the ground flora and seed banks. At Tavistock, differences in the number of species in the seed bank and ground flora of Bradford Plan sub-units of increasing age is shown in Figures 6.4b. and 6.4c. The number of species in the ground flora declines with increasing age but this trend is not apparent in the seed bank, due to the relatively young age (27 years) of the oldest sub-units.

At Werrington, the number of species in the seed bank and ground flora of conifer plantations of increasing age (28 to 53 years) are shown in Figures 6.5b. and 6.5c. The number of species in the seed bank declines with increasing age, as seed bank depletion occurs, despite the increase in the number of ground flora species.

Cutting of abandoned coppice was associated with a large increase in the ground flora and seed bank diversity only at Buckley Wood, a basic site where seed bank depletion had not occurred. At the acidic sites (Yarner Wood and Blanchdown Wood) the response to cutting was limited by a combination of species poverty and seed bank depletion.

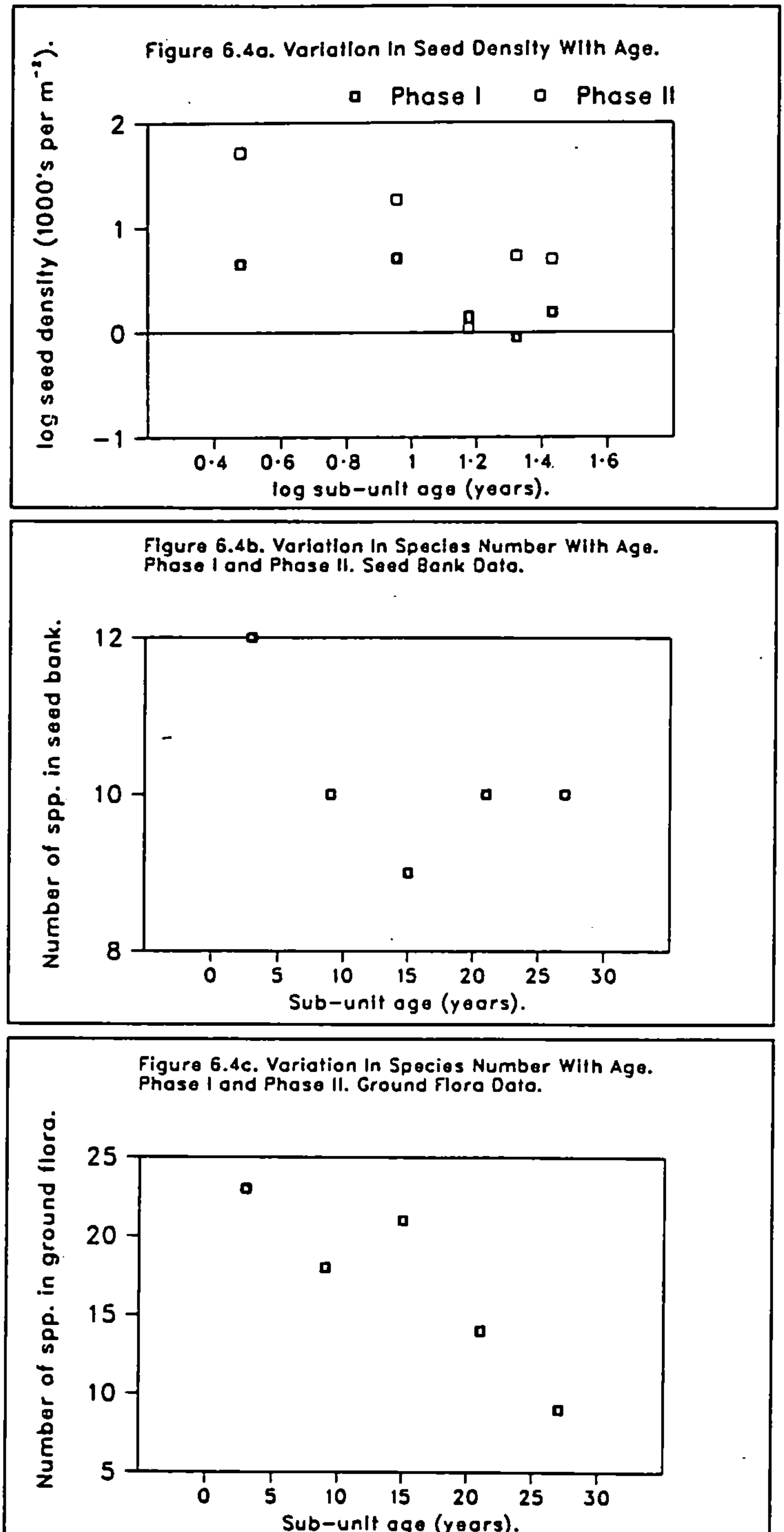


Figure 6.4. Seed bank and ground flora trends with age for Bradford Plan sub-units at Blanchdown and Grenoven Woods on the Tavistock Woodlands Estate.

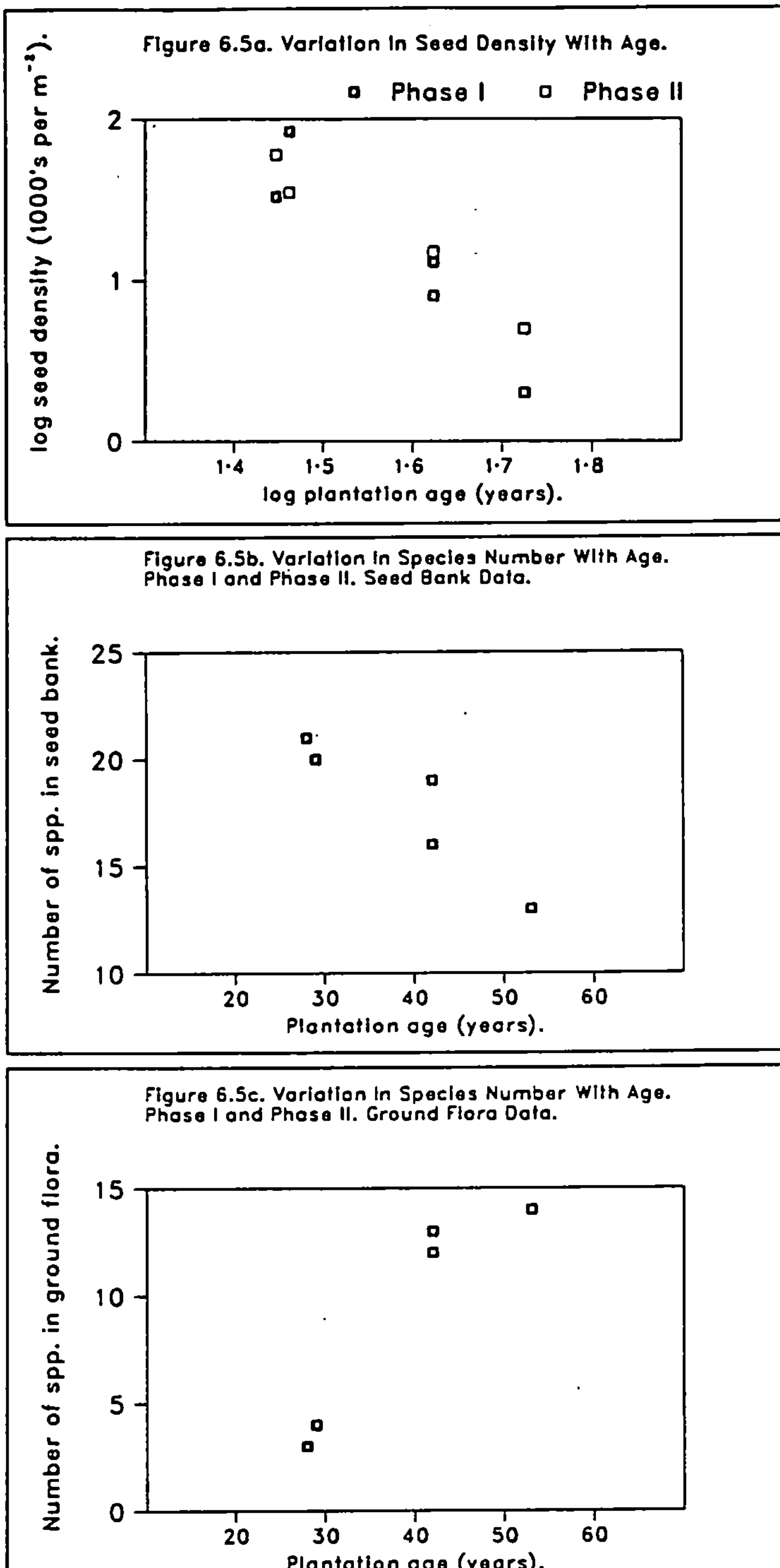


Figure 6.5: Seed bank and ground flora trends with age for conifer plantations on the Werrington Park Estate.

At the Longleat Estate, the increase in the number of species present in the seed bank and ground flora in response to opening of the canopy was similar on basic soils (thinned oak stands) and on more acid soils (uneven-aged conifers). The difference in the number of ground flora species in the open and closed stands for both conifers and broadleaves was much greater than the difference in the number of seed bank species. This is because the difference in the light environment between the open and closed stands has an immediate effect on the ground flora. The conifer stands were 18 and 24 years old; the broadleaved stands were 40 years old. This is not long enough for seed bank depletion to have occurred in the closed stands.

6.3. COMPARISON WITH OTHER STUDIES

Similar results, in terms of seed densities and species compositions, have been obtained in other studies of forest and woodland seed banks, for example Granstrom (1988) found very high densities of *Calluna vulgaris* on afforested heathland sites in Sweden. He recorded densities of up to 26600 seeds.m^{-2} in the top 6 cm of mineral soil of Norway spruce (*Picea abies*) plantations. *Carex pilulifera* and *Juncus spp.* were also abundant in the seed banks. *Calluna vulgaris* was also by far the most abundant species in the soil of conifer plantations in upland Britain studied by Hill and Stevens (1981). Other species which occurred frequently included *Carex spp.*, *Galium saxatile* and *Juncus spp.*

Table 6.2. shows estimated buried viable seed densities reported for a number of studies in coniferous and broadleaved forests and plantations. The results of different studies are not directly comparable, since experimental methods vary greatly between

Table 6.2. Estimated buried viable seed densities (seeds.m^{-2}) for coniferous and broadleaved forests. Number of species recorded in the seed bank are shown in brackets.

Source	Stand type	Age (years)	No.seeds .m^{-2}	No. of species	Depth of core
Oosting and Humphreys (1940)	Shortleaf pine	15	12714	(33)	14 cm
	Shortleaf pine	33	16267	(29)	
	Shortleaf pine	58	1393	(31)	
	Shortleaf pine	85	8339	(29)	
	Shortleaf pine	112	2839	(32)	
Olmsted and Curtis (1947)	White pine	70	1616	(11)	-
	White pine	80	0	(0)	
Livingston and Allessio (1968)	White pine	80	3365	(16)	11 cm
Kellman (1970)	Douglas fir-hemlock	100	1016	(19)	10 cm
Kellman (1974)	Douglas fir-hemlock	12	206	(16)	10 cm
		6	2612	(16)	
Johnson (1975)	Black spruce	180	0	(0)	10 cm
	White spruce	100	0	(0)	
	Jack pine	100	0	(0)	
Strickler and Edgerton (1976)	Grand fir	130	421	(12)	4 cm
	Grand fir	150	1863	(21)	
	Grand fir	175	3447	(31)	
Moore and Wein (1977)	Birch-maple	90	3400	(-)	10 cm
	Maple-beech	90	1950	(-)	
	Maple-fir	90	1230	(-)	
	Spruce-pine	90	580	(-)	
	Spruce	90	370	(-)	
Whipple (1978)	Spruce-fir	325	53	(4)	5 cm
	Lodgepole pine	325	3	(1)	
Brown and Oosterhuis (1981)	Abandoned coppice	30-40	1844	(19-32)	5 cm
Hill and Stevens (1981)	Sitka spruce	5-10	5384	(9)	10 cm
	Sitka spruce	17-18	5078	(22)	
	Sitka spruce	29-30	3549	(13)	
	Sitka spruce	41-43	1520	(11)	
Piroznikow (1983)	Lime-hornbeam-oak	mature	190 24	(32)	8 cm
Petrov and Palkina (1983)	Oak-lime	90	6500	(8)	10 cm
	Norway spruce	40	6800	(26)	
Pratt et al. (1984)	Ponderosa pine	90	13052 14463	(46)	10 cm
Conn et al. (1984)	Spruce	mature	672	(4)	15 cm
Petrov (1987)	Oak	160-180	1100	(18)	10 cm
Staaf et al. (1987)	Beech	90-100	2173	(8-24)	5 cm
Granstrom (1988)	Norway spruce	30	19112	(18)	6 cm
	Norway spruce	35	30083	(10)	
	Norway spruce	64	16674	(6)	
	Norway spruce	73	20172	(9)	

studies. For example, there are differences in sample size, sample number, surface area sampled, depth of soil sampled and time for which seed germination from soil samples was recorded. However, the results do give an indication of the range of seed densities and numbers of species occurring in the seed banks of a range of forest types.

Seed numbers are generally low in undisturbed or old-growth forests (Oosting & Humphreys, 1940; Olmsted & Curtis, 1947; Livingston & Allessio, 1968; Kellman, 1970, 1974; Johnson, 1975; Strickler & Edgerton, 1976; Whipple, 1978; Staaf et al., 1987; Piroznikow, 1983; Petrov & Palkina, 1983; Conn et al., 1984, Petrov, 1987).

Low numbers of viable seeds have also been reported in subarctic and arctic forest soils (Johnson, 1975; Leck, 1980; Archibold, 1984; Conn et al., 1984). This may, however, be related to the predominance in the seed banks of species with short-lived seeds, such as *Picea spp.* and *Empetrum nigrum.*

High seed densities were reported in a 90 year-old stand of ponderosa pine (*Pinus ponderosa*) in east-central Washington (Pratt et al., 1984). However, seeds of *Stellaria media, Poa pratensis* and *Cerastium vulgatum* accounted for over 50% of the seed bank, which suggests that recent disturbance had occurred.

Several studies of successional communities have recorded high densities of buried seeds in the early stages and low densities in climax forests (Oosting & Humphreys, 1940; Livingston & Allessio, 1968; Nakagoshi, 1984, 1985). A decline in seed bank density with age was also found by Hill & Stevens (1981) in conifer plantations on afforested hill pasture in upland Britain. In sitka spruce (*Picea sitchensis*) plantations in Wales, seed densities ($seeds.m^{-2}$) ranged from 5384 in 5-10 year-old plantations to 1520 in 41-43 year-old plantations. Granstrom (1988) reported seed densities ranging from 16674 to 30083 $seeds.m^{-2}$ in the soils of Norway spruce (*Picea abies*) plantations on afforested heathland in Sweden. The plantations were aged from 30 to 73 years and there was no trend for decline in seed numbers with increasing age.

In this study, as in Hill & Stevens (1981), seed densities were higher in the two young conifer plantations on the Werrington Park Estate than in the three older plantations (Figures 6.1a. and 6.5a.). The 42 year-old larch and spruce plantations had similar seed densities (Figure 6.1a.) and numbers of species in the seed bank (Figure 6.2a.). Although spruce canopies generally cast a deeper shade than larch, this particular spruce canopy is very open because of windthrow damage and spruce aphid infestation. The lowest seed density (Figure 6.1a.) occurred in the oldest plantation, a 53 year-old larch stand. This stand also had the lowest number of species in the seed bank (Figure 6.2a.).

These results provide no evidence that the presence of conifers *per se* has any effect on the seed bank over periods of 20-30 years. But for stands older than 50 years, there is a decline in seed density and number of species in the seed bank. In the oldest plantation, the seeds of a number of species were absent from the seed bank, for example *Teucrium scorodonia*, *Luzula pilosa* and *Potentilla erecta*. These are species which occurred at low densities in the seed banks of the younger plantations. Several species which occurred at high densities in the seed banks of the younger plantations, for example *Hypericum pulchrum*, *Calluna vulgaris* and *Juncus effusus* were absent or only present at low densities in the oldest plantation.

Hill & Stevens (1981) study supports the view that the seeds of many species have a certain life-span during which population decline takes place slowly, followed by a period during which seeds die out relatively quickly. A number of studies in temperate forests also provide evidence that rapid declines in seed densities occur in stands aged between 50 and 100 years. This is illustrated by data for survival of pin cherry (*Prunus pensylvanica*) and *Rubus* seeds in the soils of North American hardwood forests (Marks, 1974; Graber & Thompson, 1978). There is no evidence of exponential decline in seed density with age in the studies of Hill & Stevens (1981) or Granstrom (1987). In this study, seed densities in the Werrington conifer plantations (Figure 6.5a.) and in the Bradford Plan sub-units (Figure 6.4a.) do show exponential decline with age.

In Russia, Petrov (1987) studied the seed bank of a 160-180 year-old oak forest and found low seed densities (1100 seeds.m^{-2}). Most of the species present were typical forest species, which were also present in the ground flora. These results can be compared with those from the Yarner Wood oak forest and abandoned coppice plots, where the most abundant species in the seed banks were *Betula pendula* and *Vaccinium myrtillus*. Piroznikow (1983) also found that tree seeds, mainly *Carpinus betulus* and *Betula spp.*, and seeds of forest herbs such as *Oxalis acetosella* were abundant in the seed bank of a mature lime-hornbeam-oak forest in Poland.

Buried seed densities of 6500 seeds.m^{-2} for a 90 year-old oak-lime forest and 6800 seeds.m^{-2} for a 40 year-old Norway spruce (*Picea abies*) plantation were reported by Petrov & Palkina (1983). *Hypericum perforatum*, although absent from the ground flora, was the most common species in the seed bank of the oak-lime forest, accounting for 60% of the seeds present in the 0-10 cm layer. *Betula* seeds were also abundant. These results can be compared with those from the Lindridge Estate abandoned coppice and conifer plots, where *Hypericum perforatum* and *Betula spp.* were the most abundant species in the seed banks.

Seed densities in the abandoned coppice plots were low at Buckley and Yarner Woods (1920 and 4360 seeds.m^{-2} respectively in the 0-5 cm layer). More seeds were present in the abandoned coppice at Blanchdown Wood (18120 seeds.m^{-2} in the 0-5 cm layer) but this was due mainly to high densities of *Calluna* seeds. Numbers of species present in the seed banks of abandoned coppice were low at Blanchdown and Yarner Woods (9 and 7 respectively, see Table 6.1a.) and lower in the abandoned coppice than in the felled area at Buckley Wood (25 compared with 36, see Table 6.2a.). Seed bank depletion has occurred in these woods after periods of neglect of over 50 years. The number of species in the seed bank at Buckley Wood is still relatively high but few species remain in the seed banks at Blanchdown and Yarner Woods. Harris & Kent (1987b), referring to the abandoned coppice at Blanchdown Wood, drew the similar conclusion that "the potential for ground flora recovery no longer exists in the seed bank".

Brown & Oosterhuis (1981) studied the seed banks of five abandoned coppice woods in Essex and Suffolk, last coppiced 30-40 years ago. They found a mean seed density of 1844 seeds.m^{-2} in the 0-5 cm layer. Despite the low seed density, the potential for ground flora recovery remained, since there was still a high number of species present in the seed banks (19-23 species).

6.4. SPECIES RECORDED IN GERMINATION TESTS BUT EXCLUDED FROM RESULTS

Contaminants

A number of contaminant species germinated in the control trays, as shown in Table 6.3. *Senecio vulgaris*, *Epilobium spp.*, *Sonchus spp.* and *Taraxacum officinale* were frequently recorded. These are typical weed species, with wind-dispersed seeds. These species were deleted from the results of the seed bank surveys, since it was not possible to tell whether their occurrence in the samples was genuine. A number of other species, not characteristic of woodlands, occurred infrequently in the samples but were not recorded in the control trays during the phase I germination tests, for example *Anagallis arvensis*, *Chenopodium album*, *Matricaria matricarioides* and *Polygonum spp.* These species are common agricultural weeds which may have been present in the samples and could have originated from fields near the sample plots. However, during the phase II germination tests, these species were all recorded as contaminants in the shade tunnel and were therefore deleted from the phase II results.

Several other non-woodland species were recorded in the samples, particularly from Buckley Wood, for example *Buddleja davidii* and *Antirrhinum majus*. These were genuinely present in the samples and not contaminants. It is likely that they are garden escapes.

Table 6.3. List of contaminant species recorded in the control trays.

Species
Anagallis arvensis
Chenopodium album
Coronopus didymus
Crepis capillaris
Epilobium spp.
Hieracium agg.
Lolium perenne
Matricaria matricarioides
Medicago spp.
Picris echioides
Polygonum aviculare
Polygonum persicaria
Sagina apetala
Salix caprea
Senecio vulgaris
Sonchus asper
Sonchus oleraceus
Spergula arvensis
Taraxacum officinale
Trifolium dubium

Species growing from vegetative parts

A number of species sprouted from root fragments, rhizomes, bulbs and other perennial plant parts present in the samples. Some of these species also germinated from seed, for example *Vaccinium myrtillus*. No attempt was made to record the number of sprouting vegetative parts present in the samples.

Ferns

Although many ferns rely mainly on vegetative spread in order to maintain or increase their population sizes, it is likely that the spores of ferns can survive in the soil. Ferns such as *Athyrium filix-femina* and *Dryopteris dilatata*, grew from the soil samples but were not included in the results.

Related species

Since it was not practical to grow on all the seedlings, particularly when large numbers of seedlings appeared at once, for example in the case of *Juncus*, *Hypericum* and *Carex spp.*, related species with similar seedlings were counted together. In some cases, seedlings of related species were distinguishable but only present in small numbers, for example *Juncus bufonius*, *Hypericum hirsutum* and *Hypericum montanum*; these species were not counted separately.

6.5. DIFFERENCES IN SEED DENSITIES AND SPECIES COMPOSITIONS BETWEEN THE PHASE I AND PHASE II SAMPLES

Estimated viable seed densities in the 0-5 cm layer and numbers of species present at the five study sites from the phase I and phase II samples are shown in Table 6.4.

Table 6.4. Estimated viable seed densities (seeds.m^{-2}) in the 0-5 cm layer of soil at the five study sites from the phase I and phase II samples. Numbers of species in the seed banks are shown in brackets.

	phase I		phase II	
Tavistock Woodlands Estate				
Cut coppice 2 yrs	490	(4)	1400	(4)
Abandoned coppice 70 yrs	2470	(2)	18120	(6)
Bradford-Plan units				
I 27 yrs	1563	(9)	5000	(8)
II 21 yrs	900	(10)	5400	(7)
III 15 yrs	1425	(8)	1100	(5)
IV 9 yrs	5125	(9)	18700	(7)
V 3 yrs	4475	(9)	51900	(12)
Werrington Park Estate				
Sitka spruce 28 yrs	32990	(20)	59800	(12)
Sitka spruce 29 yrs	83900	(19)	34940	(13)
Sitka spruce 42 yrs	7730	(18)	12520	(12)
Japanese larch 42 yrs	13360	(15)	14540	(11)
European larch 53 yrs	2220	(11)	4920	(13)
Lindridge Estate				
Douglas fir 20 yrs	3910	(30)	3880	(18)
Hybrid larch 20 yrs	2580	(17)	4400	(21)
Felled area 25 yrs	1780	(25)	1800	(17)
Abandoned coppice 70 yrs	1900	(14)	1920	(11)
Longleat Estate				
Even-aged conifers 24 yrs	3060	(6)	35980	(10)
Uneven-aged conifers 18 yrs	1020	(12)	23020	(10)
Managed oak 40 yrs	1560	(12)	12820	(21)
Unmanaged oak 40 yrs	2070	(10)	10920	(17)
Yarner Wood				
Cut coppice 20 yrs	-	-	300	(8)
Abandoned coppice 70-80 yrs	-	-	4360	(7)
Birch woodland 80-90 yrs	-	-	3080	(6)
Oak woodland 140 yrs	-	-	2900	(8)

6.5.1. Tavistock and Longleat Sites

Seed densities in the 0-5 cm soil layer were higher for the phase II samples than for the phase I samples at both the Tavistock and Longleat Estates. At Tavistock, seed densities for the youngest B-Plan sub-units and the abandoned coppice were in the 10000's in the phase II samples compared with the 1000's in the phase I samples and in the 1000's rather than the 100's in the older B-Plan units and the cut coppice. The phase I and phase II samples were collected in June and July in 1988 and 1989 respectively.

At Longleat, estimated seed densities (seeds.m^{-2}) were in the 10000's in the phase II samples compared to the 1000's in the phase I samples, in all the stands sampled. The phase I and phase II samples were collected in May and June in 1988 and 1989 respectively. Therefore annual fluctuations in seed inputs could have accounted for some of the difference in seed densities between the phase I and phase II samples from both sites but the effect of seasonal variation should not have been significant. Germination was recorded over a twelve month period for both the phase I and phase II samples from both sites.

The percentage abundance of the most common species germinating in the 0-5 cm layer in the phase I and phase II samples at the two sites is shown in Figures 6.6a. and 6.6b. The same species were common in the seed banks in both years. The higher seed densities occurring in the phase II samples were largely attributable to an increased abundance of *Calluna vulgaris*, *Juncus effusus* and other less common species.

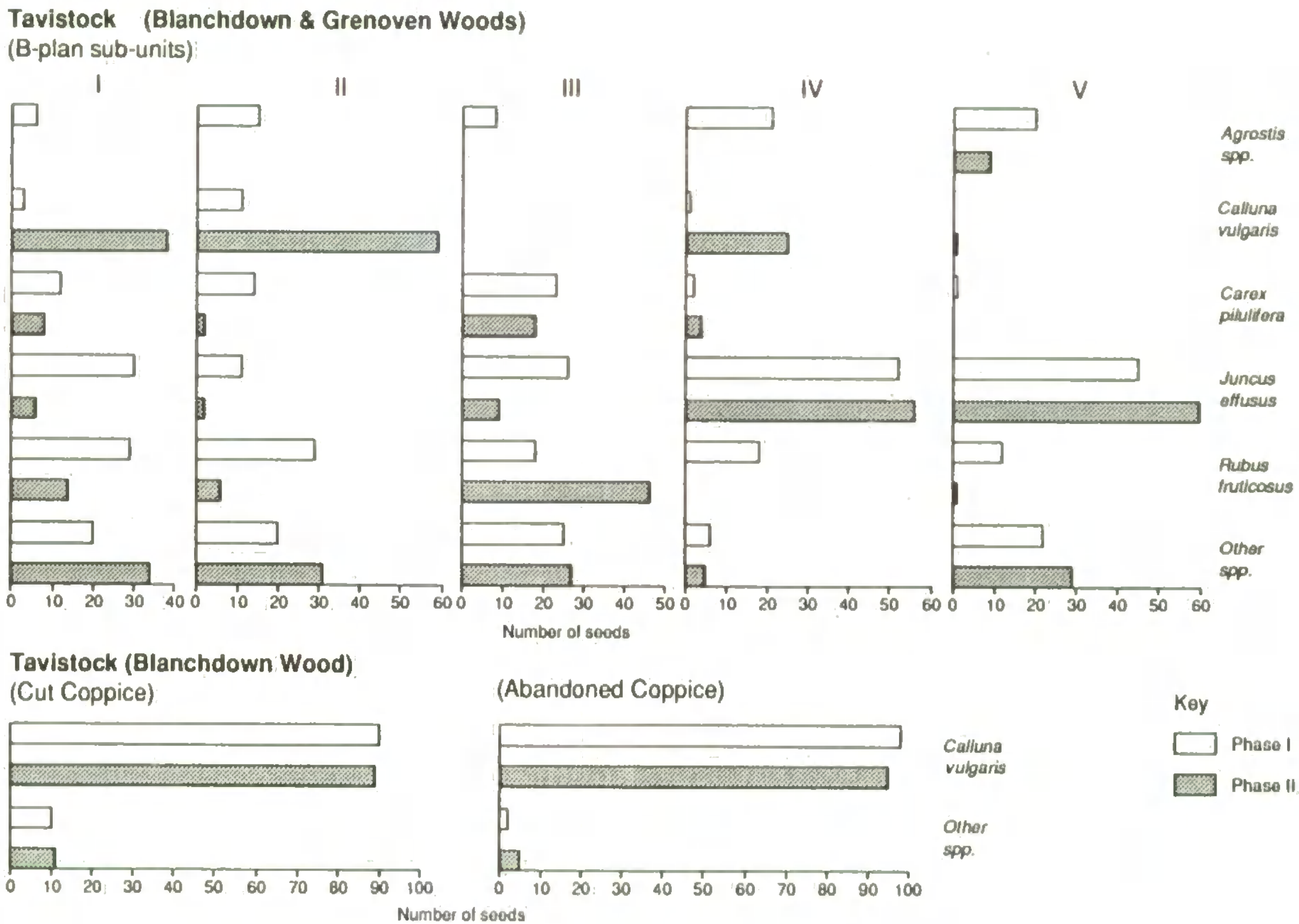


Figure 6.6a Percentage abundance of the most common species in the Phase I and Phase II soil samples (0-5 cm layer) from the Tavistock Woodlands Estate

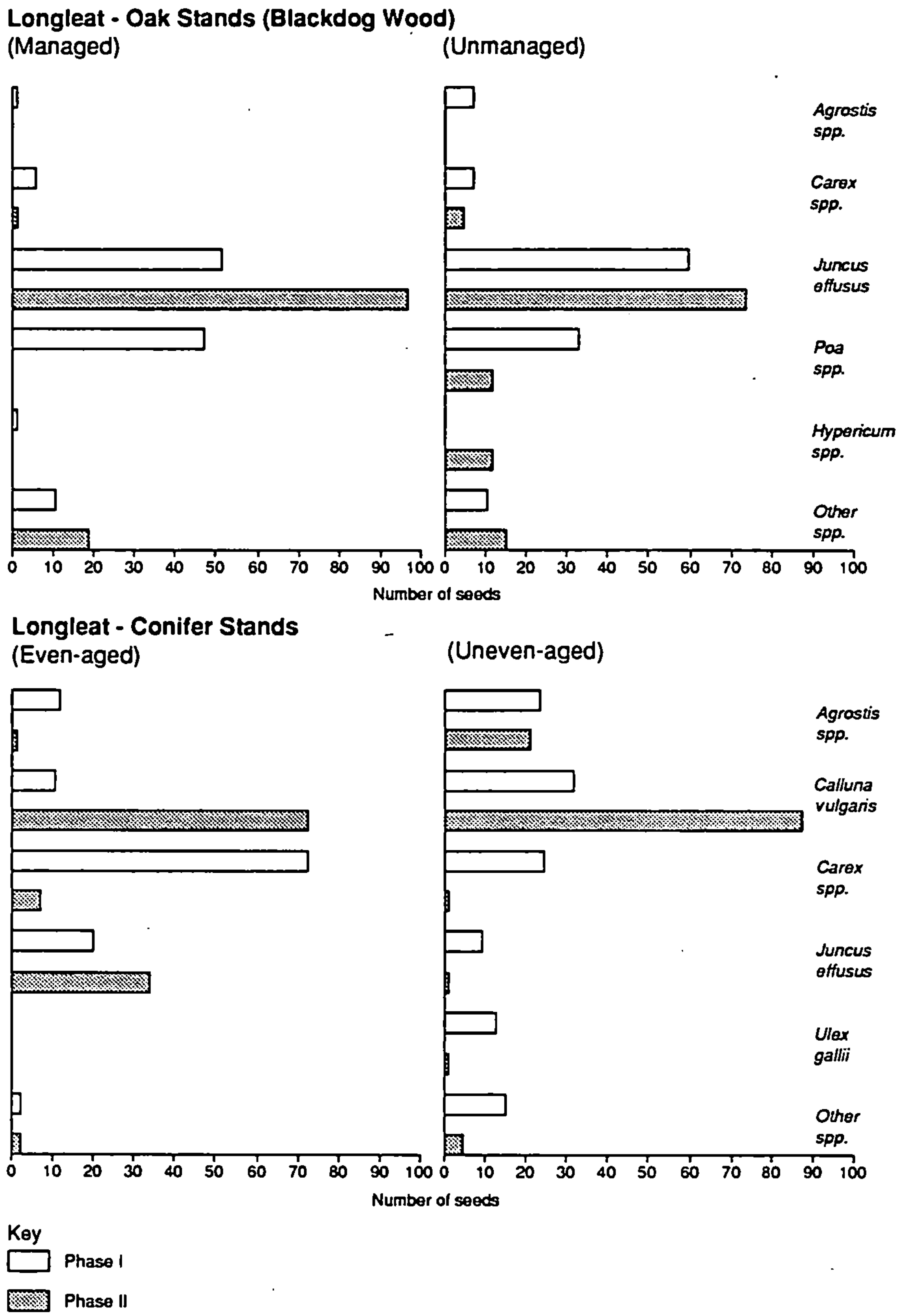


Figure 6.6b Percentage abundance of the most common species in thePhase I and Phase II soil samples (0-5 cm layer) from the Longleat Estate

The numbers of *Calluna* seeds in the phase I samples were particularly low compared with very high numbers in the phase II samples. In fact, no *Calluna* seeds were recorded in the phase I samples until the samples were more than a year old. Delayed germination of *Calluna* seeds may therefore account for a large part of the difference in seed densities in the phase I and phase II samples. Gimingham (1960) found that germination of *Calluna vulgaris* depends upon an adequate and maintained water supply. Under suitable conditions he found that up to 96% germination was obtained in two months, but in less favourable circumstances germination continued intermittently over longer periods. Since *Juncus effusus* is a wetland species, germination may also depend on a continuous water supply.

In a study of pasture seed banks, Chippindale & Milton (1934) observed germination from soil samples over a three year period. The seeds of *Calluna vulgaris* and *Juncus spp*. exhibited delayed germination. For *Calluna vulgaris*, germination in the second and third years was equivalent to that in the first. For *Juncus bulbosus* and *J. auriculatus* no germination at all took place during the first year and delayed germination also occurred in the seeds of *Juncus communis*, *J. bufonius* and *J. triglumis*. Other species which showed delayed germination included *Galium saxatile*, *Carex spp*. and *Poa spp*.

The numbers of species recorded at the species-poor Tavistock site and the Longleat conifer stands were not significantly different in the two phases. In the more species-rich Longleat oak stands, significantly more species were recorded in the phase II samples than in the phase I samples, which also suggests that germination of species other than *Calluna vulgaris* and *Juncus spp*. was unsatisfactory in the phase I samples from these sites.

Possibly, germination would have continued through the second year, but constraints of space and labour limited the time for which the samples could be kept. Delayed germination did not occur in the phase I samples from the Werrington Park and Lindridge Estates, or in the phase II samples, which were kept in the greenhouse and in the modified shade tunnel. These samples were watered more frequently, several times a day during the summer, to prevent them from drying out.

6.5.2. Lindridge and Werrington Sites

At these sites, seed densities in the 0-5 cm layer tended to be more similar in the phase II and phase I samples, although for the two youngest spruce plantations at the Werrington Park Estate seed densities in the two phases were different.

At the Werrington site, germination from the phase I samples was recorded over a period of twelve months. For the phase II samples, sampling at Castlehill plantation (the 29 year-old spruce and 53 year-old larch stands) was not carried out until March 1990, so germination from these samples was only recorded over a six month period. Phase II sampling at Rough Hill plantation (the 28 and 42 year-old spruce and the 42 year-old larch stands) was carried out in May and June 1989 and germination was recorded over a period of twelve months.

For the 29 year-old spruce plantation, estimated seed densities in the 0-5 cm layer were lower in the phase II than the phase I samples, possibly due to the shorter period of time over which germination was recorded. However, for the 28 year-old spruce plantation, when the recording period for germination from both sets of samples was twelve months, estimated seed densities were much higher in the phase II than the phase I samples. *Juncus effusus* is by far the most abundant species in the seed banks of these two plantations. The seeds of this species are extremely small and are produced in very large numbers. The density of *Juncus* seeds in the soil is therefore likely to fluctuate markedly at different times.

More species germinated from the phase I samples than the phase II samples, although agricultural weeds, such as *Anagallis arvensis* and *Chenopodium album* were probably contaminants. Other than this, the species present and their abundances in the seed banks were very similar for the two phases of sampling. At the Werrington site, the only species present in the phase II samples which was not recorded in the phase I samples was *Hyacinthoides non-scripta*. At Buckley Wood, several species were present either only in the phase II samples (*Stachys sylvatica*, *Verbascum thapsus* and *Crataegus monogyna*) or the phase I samples (*Moehringia trinervia*, *Geum urbanum* and *Holcus lanatus*). Germination was recorded for a twelve month period for both the phase I and phase II samples, with the exception of the phase II samples from the Douglas fir plantation, where the recording period was six months.

Differences may have been due to annual variations, although this would only apply to the Werrington site, since the phase I and phase II samples at Buckley Wood were collected in the same year. Differences due to sampling at different times of the year would apply to both sites. Such differences have been reported in other studies, for example, Nakagoshi (1984) found a clear seasonal decrease in the number of species and seed densities in the seed banks of temperate forest stands in southwestern Japan, which were richer in November than in May. The decrease was ascribed to losses of seeds over the winter from predation and microbial attack. Pratt et al. (1984), however, reported similar seed densities and numbers of species in samples collected in the autumn and in the spring from a Ponderosa pine (*Pinus ponderosa*) community in east-central Washington. At both sites, the phase II samples were not collected until late spring/early summer, so some early germinating species may have been missed. Species such as *Geranium robertianum*, *Moehringia trinervia* and *Galium aparine* all emerge very early in the field, when temperatures are still low (Grime et al., 1981). The seeds of *Geranium robertianum* and *Galium aparine* are short-lived (Grime et al., 1988). Buried seeds of *Moehringia trinervia* have been reported in a number of forest seed bank studies (Petrov, 1977; Donelan & Thompson, 1980; Brown & Oosterhuis, 1981; Piroznikow, 1983) and are therefore likely to be relatively long-lived. Other species with transient seed banks (Thompson & Grime, 1979) such as *Mercurialis perennis*, *Lamiastrum galeobdolon*, *Hyacinthoides non-scripta*, *Anemone nemorosa* and *Oxalis acetosella* also germinate at low temperatures in the late winter/early spring. *Geranium robertianum* and *Oxalis acetosella* were recorded in the phase I samples from the Werrington site, which were collected in October and chilled artificially. These two species were not recorded in the phase II samples which were collected in May. *Moehringia trinervia* was recorded in the phase I samples from Buckley Wood which were collected in April, but not in the phase II samples, which were collected slightly later, in May and June. However, *Moehringia* *trinervia*, *Galium aparine* and *Geranium robertianum* were all present in the phase II samples from the Longleat Estate, which were collected in June.

6.6. CONCLUSION

In this chapter, the results of the phase I and phase II seed bank surveys at each of the five sites have been discussed. The declines in seed density with increasing canopy age observed at two of the sites (Figures 6.4a. and 6.5a.) stimulated an interest in factors responsible for seed bank depletion in woodland soils. A study was carried out to investigate the role of soil fungi in seed decay. This study is described in chapter seven.

CHAPTER SEVEN : THE INFLUENCE OF SOIL- AND SEED-BORNE FUNGI AND FUNGAL INHIBITORY AGENTS IN SEED COATS ON SEED DECAY

7.1. INTRODUCTION

The factors which are responsible for depletion of seeds from soil seed banks are not well understood. Several studies have investigated weed seed longevity in agricultural soils, by measuring the decrease in viable seed numbers over time. These have indicated that a constant percentage of seeds is lost through death and germination each year, resulting in an exponential decay curve (Roberts, 1962, 1970). Depletion rates over a six year period in cultivated and undisturbed soils were compared by Roberts & Dawkins (1967). They found that a greater but still constant percentage of seeds is lost each year in cultivated soils; thus disturbance is associated with higher rates of depletion.

Fewer studies have investigated the survival of seeds in forest soils. Granstrom (1987) studied seed viability of a number of tree and shrub species during a five year period of burial in the soil of a coniferous forest in Sweden. The patterns of depletion did not indicate a constant rate of depletion. In agricultural soils, the main cause of seed depletion is thought to be germination and annual losses are substantial even for species with potentially long-lived seeds. In Granstrom's (1987) study, the seeds of some species remained dormant but viable in the soil for the entire five year period, so losses were minimal.

In this study, data presented in chapter six indicate that, over longer periods of time, exponential declines in seed densities may also occur in forest soils. At the Werrington Park Estate, for conifer plantations over an age range of 28 to 53 years, seed densities in the 0-5 cm soil layer display the straight line on a log-log plot characteristic of an exponential decay curve (Figure 6.5a.). To a lesser extent, at the Tavistock Woodlands Estate, for the phase II samples, seed densities in the 0-5 cm soil layer of Bradford Plan sub-units also exhibit exponential decline over an age range of 3 to 27 years (Figure 6.4a.).

Seed longevity and mortality is discussed by Cavers (1983). The main causes of mortality of seeds in the soil are germination, loss of viability (Roberts, 1970) and predation. Another possible cause of seed depletion is fungal and/or microbial attack; for example Roberts (1970) stated that dormant seeds remain viable in the soil "until death from fungal attack or other causes ensues." Granstrom (1987) observed fungal degradation of the seed coats of *Betula pendula*, *Sorbus aucuparia*, *Vaccinium myrtillus* and *V. vitis-idaea* after five years of burial in the soil. Although the viability of the seeds was not affected, loss of the protective pericarp and testa would render the embryo vulnerable to attack by soil microorganisms.

The seeds of certain plant species are attacked by fungi, others are not (Ferenczy, 1956; Halloin, 1983). A number of studies have shown that the seed coats of certain species contain substances, usually phenolic compounds, which inhibit the growth of seed-decomposing fungi and bacteria. These studies have been concentrated on the seeds of commercially important agricultural crop and associated weed species, such as cereals (Srivastava & Mishra, 1971; Picman et al. 1984), beans (Roy & Sharma,

1982) and velvetleaf (*Abutilon theophrasti*), a serious weed of row crops in the U.S.A. (Kremer et al., 1984; Kremer, 1986; Paszkowski & Kremer, 1988).

Halloin (1983) observed that large, cultivated edible seeds such as those of cereals and legumes, generally lack deterioration resistance mechanisms. Seeds of weeds and wild varieties of cultivated species tend to have superior resistances to deterioration. He suggested that this is because characteristics which confer resistance have been bred out of edible seed varieties. For example, the presence of flavanols and tannins in seed coats would be undesirable because they impart astringency to foods.

7.2. EXPERIMENTS

7.2.1. Aim of the study

The aim of the study was to investigate the susceptibility of different seeds to attack by seed-decomposing fungi. Experiments were carried out to assess the fungal inhibitory properties of seeds and seed coat extracts against a number of fungi typically found in woodland soils. The seeds used were those of ground flora species rather than those of trees or shrubs.

Samples of woodland soil were collected from the Werrington Park Estate conifer plantations. Fungi were isolated from diluted samples of soil, plated out on potato dextrose agar. The aim was to determine which fungi are of common occurrence. Species from the following genera were present: *Mucor*, *Penicillium*, *Trichoderma* and *Pythium*. Of these, *Trichoderma viride* and *Pythium sp.* were selected for the experiments, *T. viride* because it is an antibiotic-producing fungus, and *Pythium sp.* as a potential seed pathogen. Two other pathogenic fungi, *Rhizoctonia solani* and *Botrytis cinerea* were also investigated.

7.2.2. Experiment 1

Aim

The aim of this experiment was to test the resistance of seeds of six woodland ground flora species to fungal attack.

Method

Species tested included *Allium ursinum*, *Hyacinthoides non-scripta* and *Anemone nemorosa*, which have large, short-lived seeds and *Digitalis purpurea*, *Hypericum pulchrum* and *Silene dioica*, which have small, long-lived seeds. The seeds were obtained from a supplier with the exception of the *Anemone* seeds which were collected locally.

Seeds were surface sterilized (five minutes in 0.2% sodium hypochlorite solution, followed by three rinses in sterile distilled water). The seeds were then placed onto Petri plates containing malt agar medium, in small groups forming a ring around the centre of the plate. Small discs (5 mm diameter) cut from agar cultures of the fungi were inoculated onto the centre of each of the plates, which were incubated at 25°C (Figure 7.1a.). The plates were inspected after two, four and six days to monitor the growth of the inoculated fungi. The experiment was repeated using untreated seeds

what sp. was used?

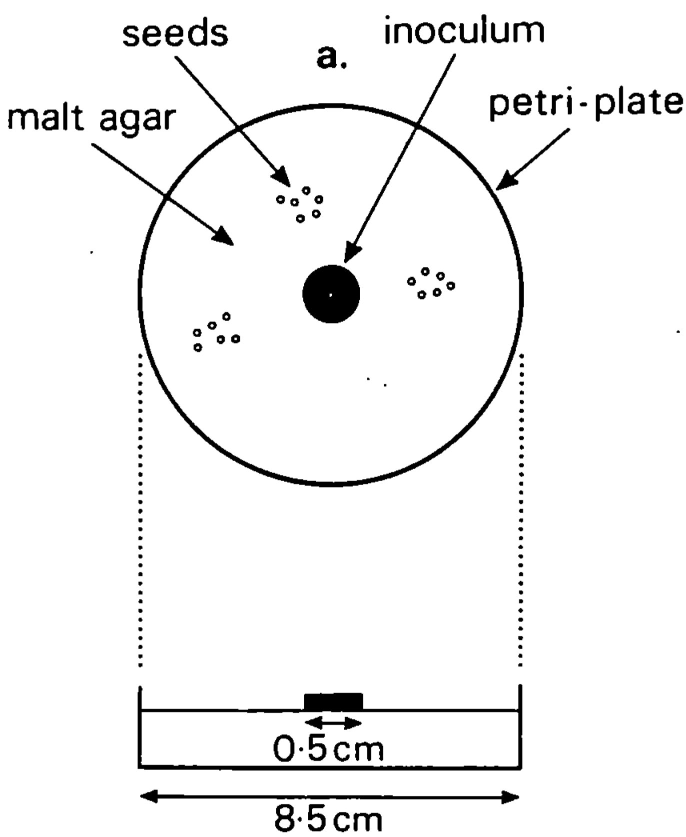


Figure 7.1a.

Experiment 1. Testing the resistance of seeds of woodland ground flora species to fungal attack.

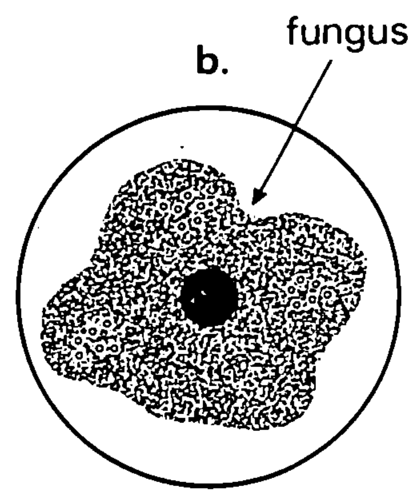


Figure 7.1b.

No inhibition of inoculated fungus by surface-sterilized seeds after six days incubation at 25°C.

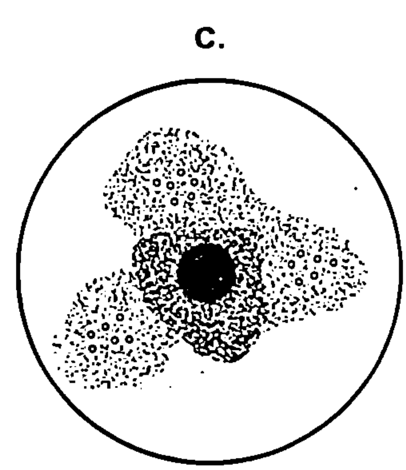


Figure 7.1c.

Inhibition of inoculated fungus by growth of seed-borne fungi on untreated seeds after six days incubation at 25°C.

to investigate whether fungi present on the seeds inhibited the growth of the inoculated fungi.

Results

For surface-sterilized seeds, there was no evidence of inhibition of any of the fungi by any of the species of seeds tested (Figure 7.1b.). For untreated seeds growth of seed-borne fungi inhibited the growth of the inoculated fungi (Figure 7.1c.). Particular fungi were associated with different seeds. *Rhizopus* with *Allium*, *Mucor* with *Digitalis* and *Silene*, and *Penicillium* with *Hyacinthoides* and *Anemone*.

Discussion

Surface-sterilized seeds are apparently not resistant to colonisation by fungi. Untreated seeds had fungi associated with them which inhibited the growth of the inoculated fungi. The presence of fungi on seeds has been reported in a number of studies, for example Kirkpatrick & Bazzaz (1979), Mishra & Srivastava (1977), Kanapathipillai & Hashim (1981), Kremer et al. (1984).

The seed coat acts as a physical barrier, seeds are readily attacked by fungi if the seed coat is damaged or removed (Kremer et al., 1984; Picman et al., 1984).

7.2.3. Experiment 2

Aim

The aim of this experiment was investigate the inhibition of seed-borne fungi on the seeds of six woodland ground flora species by antibiotic substances produced by *T.*

viride. The presence of seed-borne fungi was demonstrated in Experiment 1. A number of fungi present in the soil can inhibit the growth of other fungi by producing antibiotic substances. *T. viride* is an example of such a fungus.

Method

Seeds tested included *Allium ursinum*, *Hyacinthoides non-scripta*, *Anemone nemorosa*, *Digitalis purpurea*, *Hypericum pulchrum* and *Silene dioica*.

Sterile extracts of *T. viride* were prepared by seeding a broth of malt extract with spores of *T. viride*, which was shaken for seven days. This was filtered crudely through Whatman No. 1 paper, followed by membrane filtration to produce a sterile solution. The seeds were treated with the extract and placed onto Petri plates containing malt agar medium. An equal number of plates were prepared using untreated seeds to act as a control (Figure 7.2a.). The plates incubated at 25°C and checked after two, four and six days to monitor the growth of any seed-borne fungi.

Results

Treatment with extracts of *T. viride* was found to inhibit the growth of the seed-borne fungi on all seeds tested (Figure 7.2b.). Seed-borne fungi grew on untreated seeds (Figure 7.2c.).

Discussion

Although this experiment did not attempt to reproduce natural conditions, it demonstrated possible interactions between soil fungi and seed-borne fungi.

a.

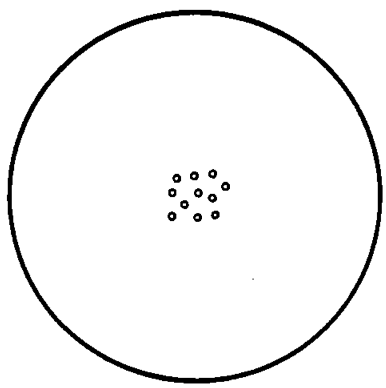


Figure 7.2a.

Experiment 2. Investigating the inhibition of seed-borne fungi on the seeds of woodland ground flora species by antibiotic substances produced by *Trichoderma viride.*

b.

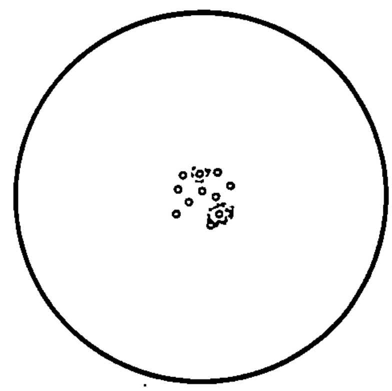


Figure 7.2b.

Seeds treated with extracts of *Trichoderma viride*: Inhibition of seed-borne fungi after six days incubation at 25°C.

c.

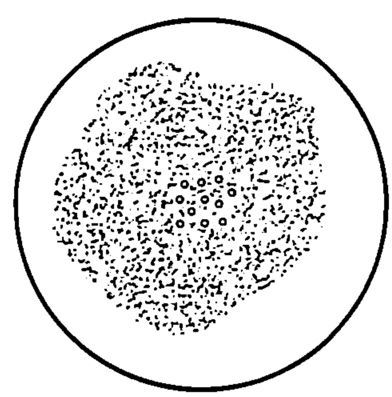


Figure 7.2c.

Untreated seeds: Growth of seed-borne fungi has taken place after six days incubation at 25°C.

7.3.4. Experiment 3

Aim

The aim of this experiment was to investigate the presence of fungal inhibitory agents in seed coat extracts from the seeds of four woodland ground flora species.

Method

Seeds tested included *Allium ursinum*, *Hyacinthoides non-scripta*, *Digitalis purpurea* and *Hypericum pulchrum*. Fungi tested were *T. viride*, *R. solani*, *Pythium sp.* and *B. cinerea*.

The method was developed from techniques used in similar studies (Roy & Sharma, 1982 and Christensen et al., 1988). Seeds (0.5 g) were surface-sterilized, then shaken with 100 ml sterile distilled water overnight and the liquid decanted and filtered through Whatman No. 4 paper. The filtrate was concentrated in a water bath at 50°C to a final volume of 5 ml. This process was repeated until sufficient seed coat extract was obtained.

A number of studies have used organic solvents to obtain seed coat extracts but, as pointed out by Paszkowski & Kremer (1988), extracts obtained in this way are not representative of natural conditions where chemicals are leached out of seeds by water.

For the fungal toxicity tests, 2 ml of seed coat extract was added to each Petri plate containing malt agar medium. The extract was added to the plates through micro-filter membranes, to prevent any toxic effects caused by contamination. For controls, 2 ml of sterile distilled water was used instead of the extract. Discs of the test fungus were inoculated onto the centre of each plate and the plates incubated at 25°C (Figure 7.3a.). For *Hyacinthoides non-scripta* and *Digitalis purpurea* extracts, 20 replicate plates and 20 control plates were prepared for each fungus. For *Allium ursinum* and *Hypericum pulchrum* extracts, 10 treated and 10 control plates were prepared for each fungus.

The growth of the fungus was recorded by measuring colony diameter after two, four and six days (Figure 7.3b.). The Petri plates were 8.5 cm in diameter, so this measurement represents maximum possible growth.

Results

For each of the four seed coat extracts, t-tests were carried out to indicate whether differences in the growth rates of the four fungi on the treated and control plates were significant after two, four and six days. The mean colony diameters and the results of the t-tests are shown in Tables 7.1. and 7.2. For *T. viride*, *R. solani* and *Pythium sp.*, no obvious inhibitory effects were detected for any of the seed coat extracts. The rates of growth were different for the different fungi. *T. viride* grew particularly vigorously, normally reaching maximum growth within four days.

There was, however, inhibition of *B. cinerea* by extracts from *Digitalis purpurea* and *Hypericum pulchrum*. Growth of the fungus on the treated and control plates was not significantly different after two days, but after four and six days, fungal growth was slower on the treated plates. This effect was not found with extracts from *Hyacinthoides non-scripta* or *Allium ursinum*; for these species there were no

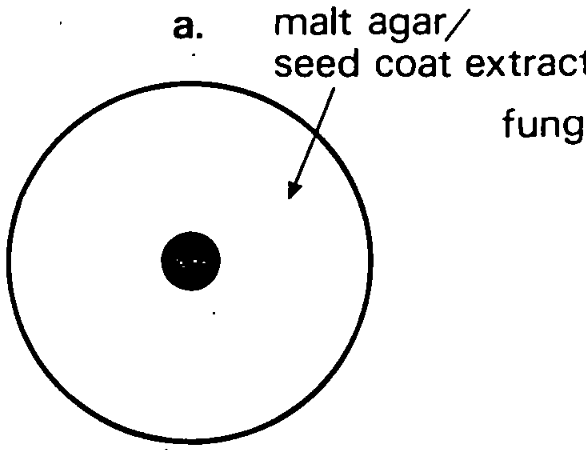


Figure 7.3a.

Experiment 3. Investigating the presence of fungal inhibitory agents in seed coat extracts from the seeds of woodland ground flora species.

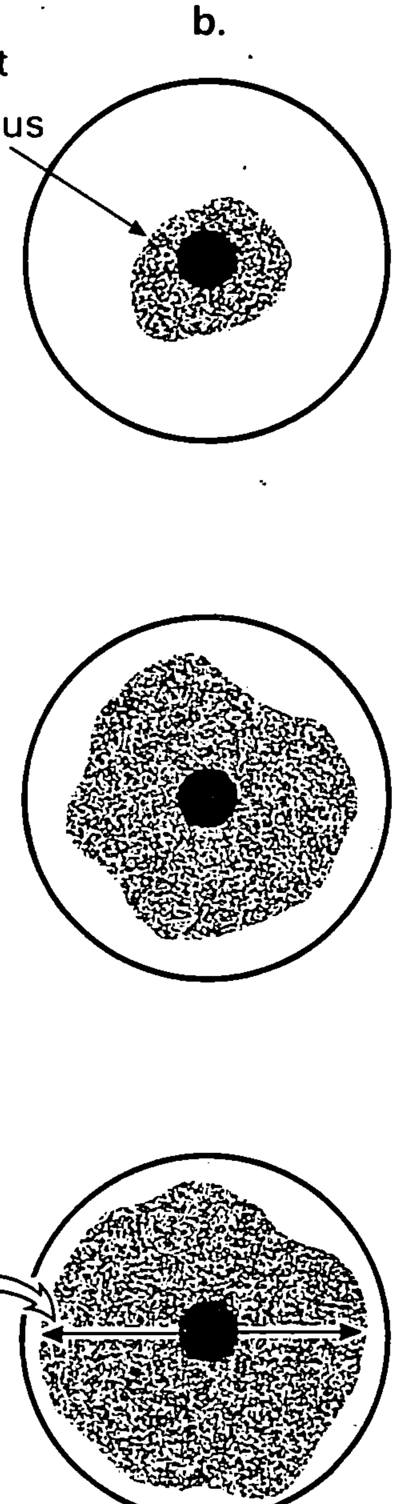


Figure 7.3b.

Growth of fungus after two, four and six days incubation at 25°C.

Table 7.1. Mean colony diameter (x ± s.d.) of test fungi on Treated (T) and Control (C) plates after two, four and six days incubation at 25°C, in an experiment to investigate the inhibitory properties of seed-coat extracts of four woodland ground flora species on the growth of four test fungi.

a. *Hyacinthoides non-scripta* (n = 20).

Test fungi	Two days		Four days		Six days	
	T	C	T	C	T	C
T. viride	7.9 ± 0.5	8.0 ± 0.4	8.4 ± 0.2	8.5 ± 0.1	-	-
R. solani	3.0 ± 0.4	3.2 ± 0.5	6.0 ± 0.5	6.2 ± 0.3	8.1 ± 0.3	8.3 ± 0.2
B. cinerea	1.9 ± 0.7	2.0 ± 0.8	6.8 ± 0.5	7.1 ± 0.7	8.2 ± 0.4	8.2 ± 0.3
Pythium sp.	2.4 ± 0.1	2.3 ± 0.3	6.6 ± 0.5	6.7 ± 0.4	8.2 ± 0.5	8.3 ± 0.2

b. *Allium ursinum* (n = 10).

Test fungi	Two days		Four days		Six days	
	T	C	T	C	T	C
T. viride	7.9 ± 0.6	8.1 ± 0.4	8.2 ± 0.5	8.4 ± 0.3	-	-
R. solani	2.4 ± 0.7	2.4 ± 0.9	5.6 ± 0.5	5.4 ± 0.7	8.2 ± 0.4	8.3 ± 0.2
B. cinerea	1.7 ± 0.4	1.8 ± 0.7	5.6 ± 1.3	5.7 ± 1.4	7.1 ± 0.9	7.5 ± 1.1
Pythium sp.	2.7 ± 0.6	2.8 ± 0.5	6.3 ± 0.6	6.4 ± 0.7	8.2 ± 0.5	8.4 ± 0.2

c. *Digitalis purpurea* (n = 20).

Test fungi	Two days		Four days		Six days	
	T	C	T	C	T	C
T. viride	8.1 ± 0.4	7.9 ± 0.5	8.4 ± 0.2	8.5 ± 0.1	-	-
R. solani	2.1 ± 0.6	2.4 ± 0.8	5.7 ± 0.4	5.9 ± 0.3	8.2 ± 0.1	8.3 ± 0.2
B. cinerea	1.8 ± 0.5	2.0 ± 0.6	5.3 ± 0.9	7.5 ± 0.7	6.1 ± 1.0	8.2 ± 0.3
Pythium sp.	2.5 ± 0.6	2.7 ± 0.3	6.5 ± 0.7	6.5 ± 0.6	8.0 ± 0.4	8.1 ± 0.5

d. *Hypericum pulchrum* (n = 10).

Test fungi	Two days		Four days		Six days	
	T	C	T	C	T	C
T. viride	8.1 ± 0.5	8.2 ± 0.4	8.4 ± 0.2	8.3 ± 0.3	-	-
R. solani	1.7 ± 0.3	2.0 ± 0.3	5.9 ± 0.2	5.9 ± 0.3	8.2 ± 0.5	8.1 ± 0.4
B. cinerea	2.3 ± 0.7	2.0 ± 0.5	5.4 ± 0.8	7.7 ± 0.5	6.5 ± 0.9	7.9 ± 0.5
Pythium sp.	2.6 ± 0.5	2.7 ± 0.6	6.9 ± 0.5	6.7 ± 0.5	8.4 ± 0.2	8.2 ± 0.3

Table 7.2. Results of t-tests comparing mean colony diameter of test fungi on treated and control plates after two, four and six days incubation at 25°C, in an experiment to investigate the inhibitory properties of seed-coat extracts of four woodland ground flora species on the growth of four test fungi.

a. *Hyacinthoides non-scripta* (n = 20).

Test fungi	Two days	Four days	Six days
T. viride	N.S.	N.S.	-
R. solani	N.S.	N.S.	*
B. cinerea	N.S.	N.S.	N.S.
Pythium sp.	N.S.	N.S.	N.S.

b. *Allium ursinum* (n = 10).

Test fungi	Two days	Four days	Six days
T. viride	N.S.	N.S.	-
R. solani	N.S.	N.S.	N.S.
B. cinerea	N.S.	N.S.	N.S.
Pythium sp.	N.S.	N.S.	N.S.

c. *Digitalis purpurea* (n = 20).

Test fungi	Two days	Four days	Six days
T. viride	N.S.	N.S.	-
R. solani	N.S.	N.S.	N.S.
B. cinerea	N.S.	***	***
Pythium sp.	N.S.	N.S.	N.S.

d. *Hypericum pulchrum* (n = 10).

Test fungi	Two days	Four days	Six days
T. viride	N.S.	N.S.	-
R. solani	*	N.S.	N.S.
B. cinerea	N.S.	***	***
Pythium sp.	N.S.	N.S.	N.S.

N.S. = not significant
* = significant $P < 0.05$
*** = significant $P < 0.001$

significant differences in the growth rates of the fungus on the treated and control plates.

Discussion

Paszkowski & Kremer (1988) reported a similar lack of inhibition of *T. viride* in aqueous extracts of *Abutilon theophrasti* seeds. They suggested that this may be because *T. viride* is a potentially beneficial (to the seed) fungus since it prevents the growth of potential seed-decomposing fungi. However, Kremer (1986) found that the growth of *T. viride* was inhibited by velvetleaf seed diffusates. The lack of inhibition of *R. solani* and *Pythium sp.* (both pathogenic) may have been due to insufficient strength of the extracts. Paszkowski & Kremer (1988) reported no significant effect on the growth of fungal test species at concentrations of 25 mg seed coat per ml water, whereas concentrations of 50 and 100 mg/ml inhibited the growth of certain pathogenic fungi. Although the concentration of the extracts used in this study were ?100 50 mg seeds?/ml, intact seeds were extracted whereas Paszkowski & Kremer (1988) fractionated intact seeds into seed coats and embryos and extracted the seed coats only.

The inhibition effect detected for seed coat extracts from *D. purpurea* and *H. pulchrum* is interesting, since the seeds of these species are long-lived whereas those of *H. non-scripta* and *A. ursinum* are short-lived. It is possible that long-lived seeds have some substances in the seed coats which are toxic to seed-decomposing fungi. This interpretation of the results can only be tentative, since the effect was not detected in two out of the three pathogenic fungi tested. It is possible that higher concentrations of seed coat extracts are required to produce a detectable effect, but this would need to be tested experimentally. These could be obtained by using seed coats only, rather than intact seeds, but the separation of the testas and embryos of the small-seeded species would be laborious. Further testing is required to confirm the effect, and if fungal inhibitory agents are present, to demonstrate their role under natural conditions.

Haack et al. (1956) reported a high content of partly toxic secondary compounds in the seeds of *Digitalis purpurea*. These may, as suggested by van Baalen (1982), play a role in repelling potential predators. They may, presumably also function to protect buried seeds against seed-decomposing fungi.

7.3. CONCLUSION

It may be concluded that soil fungi do cause seed depletion in woodland soils. The experiments demonstrate the presence of seed-borne fungi on woodland seeds and examine some of the interactions which may occur between seed-borne fungi and soil fungi.

For some species, the seed coat, as well as providing a physical barrier to fungal attack, contains inhibitory substances. For the seeds tested, these substances, if present, had no effect on the growth of *T. viride*, *R. solani* or *Pythium sp.* but did inhibit the growth of *B. cinerea* under experimental conditions. This inhibitory effect was only detected in the seed coat extracts of the long-lived seeds. The vulnerability of seed coats to fungal decay may be determined by the concentration and nature of the inhibitory substances present. These substances may be absent from the seed coats of short-lived seeds, although further testing is required to demonstrate this.

In natural conditions, resistance to microbial attack, acting together with seed dormancy mechanisms may ensure longevity of buried seeds of long-lived species. The interactions between soil fungi, fungi on and in the seed coat and fungal inhibitory agents are likely to be complex and difficult to re-create under experimental conditions but are a promising subject for further study. Factors affecting the persistence of seeds in forest soils represent an important area for the future understanding of woodland seed banks and their dynamics.

CHAPTER EIGHT : DISCUSSION AND CONCLUSIONS

8.1. INTRODUCTION

The aims of the thesis were set out in chapter one. Primarily, the thesis examines the seed banks and ground flora associated with different forest and woodland types in south west England. A further aim is to assess the potential of alternative coniferous forestry systems for conserving a diverse ground flora in comparison with clear-fell systems, which generally support only a limited ground flora. In addition, the research considers ways in which forestry management systems can be modified to encourage a greater woodland ground flora diversity and ecological interest.

To fulfil these aims, six objectives were defined (see section 1.1.1.). In summary these were to:

a. Study the species composition of seed banks and ground flora associated with different types of woodland.

b. Study changes in ground flora associated with changes in forestry management practices.

c. Study changes in seed banks associated with changes in forestry management practices.

d. Examine the distribution of seeds in woodland seed banks.

e. Assess the difficulties of sampling woodland seed banks and devise improved sampling techniques.

f. Formulate guidelines for encouraging a more diverse woodland ground flora and seed bank within coniferous woodland.

This chapter reconsiders these objectives and examines the extent to which they have been achieved. The key results relating to each of the objectives are discussed. The presence and absence of species in woodland seed banks (a.) is discussed in section 8.2. In section 8.3., the effects of neglect and coniferisation on both the seed bank and ground flora are examined and the potential of uneven-aged forestry systems for maintaining a diverse ground flora and seed bank (b. and c.) is evaluated. The distribution of seeds in the soil (d.) was discussed in chapter five and is not considered further in this chapter. The problems encountered and the methods used for sampling (e.) are discussed in section 8.4. Guidelines for encouraging a more diverse woodland ground flora and seed bank (f.) are specified in section 8.5. Finally, some suggestions for further work are outlined in section 8.6.

8.2. SPECIES PRESENT IN AND ABSENT FROM WOODLAND SEED BANKS

8.2.1. Species Common in the Seed Banks

Some species were frequently present in the seed banks even though they were absent from the ground flora. This applied to species belonging to the following genera:

Juncus, Hypericum, Poa, Ulex, Rumex, Calluna, Digitalis, Carex and *Rubus*. These are all shade-intolerant species which characteristically have persistent seed banks (Types III and IV of Thompson & Grime, 1979) or permanent seed banks (Bakker, 1989). A detailed account of these seed bank types has been given in section 1.5.4. The accumulation of a seed bank of light-demanding species in the soil beneath temperate woodlands and plantations has been demonstrated in a number of studies (Thompson & Grime, 1979; Brown & Oosterhuis, 1981; Hill & Stevens, 1981; Granstrom, 1988). These seed banks are commonly assumed to be successional in origin. Mostly, this is because the species composition is similar to that of the ground flora which appears after felling (eg. Brown & Oosterhuis, 1981). Further studies are required to determine whether these species are also present in the seed rain.

With the exceptions of *Rubus* and *Ulex*, these species all have small seeds. Small seed size is one of the characteristics of seeds with persistent seed banks (see section 1.5.4.).

Tree and shrub species are generally absent from woodland seed banks (see section 8.2.2.). However, the following woody species were well represented in the seed banks at the sites studied: *Betula spp.*, *Calluna vulgaris*, *Rubus fruticosus* and *Ulex gallii*. These species are all described as having persistent (Types III and IV) seed banks by Grime et al. (1988). The seeds of *Calluna vulgaris* and *Betula spp.* are small but those of *Rubus fruticosus* and *Ulex gallii* are relatively large.

Rubus fruticosus has bird-dispersed seeds. In unmanaged woodland, the intervals between disturbances tend to be very long. Marks (1983) has argued that under such circumstances seed survival in the soil has no adaptive value unless combined with good dispersal, and has drawn parallels between *Rubus spp.* and *Prunus pensylvanica*, a North American pioneer tree which also has long-lived seeds.

The seeds of *Ulex spp.* are explosively discharged and may be dispersed by ants but dispersal is not usually over long distances. Persistence of the seeds in the soil may be associated with the hard seed coat which protects the seed from high temperatures, allowing establishment after fire (Grime et al., 1988).

8.2.2. Species Absent from the Seed Banks

Tree and shrub species

In general, tree and shrub species were poorly represented in the seed banks. Woody species present in the ground flora but absent from the seed bank are listed in Table 8.1. Seeds of *Fraxinus excelsior, Crataegus monogyna, Sambucus nigra* were present in the soil samples, but were infrequent and confined to the upper soil layers. Most of these species were also recorded in the phase I litter samples. Conifer seedlings only germinated from the litter samples. Species with large seeds such as acorns, which would have been removed when the soil was sieved, have not been included in Table 8.1.

There is evidence (Grime, cited in Thompson, 1978) that the seeds of many temperate deciduous trees are short-lived. A number of tree and shrub species, including *Corylus avellana*, *Fagus sylvatica*, *Sambucus nigra* and *Sorbus aucuparia*, are described as having transient (Type II) seed banks by Grime et al. (1988).

Table 8.1. Tree and shrub species present in the ground flora but absent from the seedbank. Species with large seeds which would have been removed by sieving (eg. *Fagus sylvatica*, *Corylus avellana*, *Castanea sativa* and *Quercus spp.*) have not been included.

Species not recorded in germination tests
Euonymus europaeus
Ilex aquifolium
Ligustrum vulgare
Prunus spinosa
Rhododendron ponticum
Rosa canina
Ruscus aculeatus
Sorbus aucuparia
Species recorded infrequently in germination tests
Crataegus monogyna
Fraxinus excelsior
Sambucus nigra

The lack of germinating seeds of tree and shrub species, (see section 1.6.3.), has also been reported in other studies of temperate forest seed banks, for example Pratt et al. (1984) estimated that tree and shrub species accounted for less than 1% of the seed bank of a ponderosa pine (*Pinus ponderosa*) community in east-central Washington. The survival of most conifer seeds is known to be of short duration (eg. Frank & Safford, 1970). In studies of coniferous forest seed banks, germination of conifer seeds is uncommon (Kellman, 1970; 1974; Strickler & Edgerton, 1976; Whipple, 1978; Hill & Stevens, 1981; Pratt et al., 1984).

Ground flora species

A number of species which were present in the ground flora were absent from the seed banks, or present infrequently and only in the upper soil layers. In Table 8.2., these species are listed and seed bank types, if known, are indicated.

Similar lists of species common in the ground flora but not germinating from soil samples have been reported for abandoned coppicewoods (Brown & Oosterhuis, 1981), conifer plantations (Hill & Stevens, 1981; Granstrom, 1982) and mature forests (Karpov, 1960; Petrov, 1977).

The species listed in Table 8.2. are mostly either vernal or shade-tolerant species which have transient (Types I and II) seed banks (Grime et al. 1988). The problems of detecting species with transient seed banks have been referred to in section 3.2.1., when the timing of sample collection was discussed.

Table 8.2. Species present in the ground flora but absent from the seed bank. Ferns have not been included. Seed bank types as defined by Thompson and Grime (1979). Source: Grime et al. (1988).

Species not recorded in germination tests	Seed bank type
Adoxa moschatellina	?
Anemone nemorosa	II
Arum maculatum	II
Bromus ramosus	II
Circaea lutetiana	II
Conopodium majus	II
Deschampsia flexuosa	I
Festuca gigantea	II
Hedera helix	?
Holcus mollis	?
Lamiastrum galeobdolon	II
Listera ovata	?
Lonicera periclymenum	II?
Melampyrum pratense	II?
Mercurialis perennis	II
Prunella vulgaris	III?
Ranunculus ficaria	II
Solanum dulcamara	II
Solidago virgaurea	I
Tamus communis	II
Species recorded infrequently in germination tests	**Seed bank type**
Euphorbia amygdaloides	?
Galium aparine	II
Geum urbanum	II
Glechoma hederacea	?
Fragaria vesca	IV?
Hyacinthoides non-scripta	II
Iris foetidissima	?
Oxalis acetosella	?
Potentilla sterilis	III/IV?
Viola riviniana	II

In some cases where the seed bank type is not known, regeneration is primarily vegetative, for example *Glechoma hederacea* often spreads rapidly by means of long, creeping stems; seed set is generally poor. *Oxalis acetosella* also regenerates mainly as a result of clonal growth, through rhizome extension. In addition, seeds are produced and have been found to be abundant in some woodland soils, although only in the upper soil layers (eg. Piroznikow, 1983; Petrov, 1977; Staaf et al., 1987; Kjellsson, 1988). It is possible that this species sometimes forms a persistent seed bank. In other studies, for example Karpov (1960), as in this study, *Oxalis* seeds have been absent or rare in the seed bank.

Other studies have also found that the grasses *Holcus mollis* (Thompson & Grime, 1979) and *Deschampsia flexuosa* (Thompson & Grime, 1979; Hill & Stevens, 1981; Granstrom, 1982) are absent from woodland seed banks, despite being present in the ground flora. *Holcus mollis* relies mainly on vegetative reproduction, producing extensive clonal stands (Grime et al. 1988). *Deschampsia flexuosa* is capable of forming large clonal patches as a result of rhizome growth but also reproduces by seed. However, since the seeds germinate in the autumn after shedding, no persistent seed bank is formed.

Some of the species listed in Table 8.2. only flower and produce seed in clearings, for example, *Mercurialis perennis* and *Anemone nemorosa*. Climbing species such as *Hedera helix*, *Lonicera periclymenum* and *Tamus communis* rarely escape the shade of their accompanying trees and shrubs, and so they seldom flower (Grime et al., 1988). Poor seed production could therefore account for the scarcity of seeds of these species in the seed bank.

High rates of predation may also explain the lack of seeds of certain species. Tree seeds form an important part of the diet of wood mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*). Seeds of *Hyacinthoides non-scripta, Mercurialis perennis, Oxalis acetosella* and *Anemone nemorosa* are also eaten by these small rodents, sometimes in considerable quantities (Watts, 1968; Gebczynska, in Piroznikow, 1983).

8.3. EFFECTS OF CONIFERISATION AND NEGLECT ON WOODLAND SEED BANKS AND GROUND FLORA

8.3.1. Seed Bank

Few of the conifer plantations studied had reached an age where significant depletion of the seed banks had occurred. However, the study provides evidence that depletion of the seed bank does take place in older stands of conifers.

One of the effects of introducing conifers to sites which previously supported broadleaves is increased soil acidity (Miles, 1978). It is possible that this reduces the longevity of buried seeds, although there is no conclusive evidence linking acid conditions with reduced seed longevity (see section 1.5.2.).

Low seed densities and species diversities were found in neglected coppice. The species present were those with short-lived seeds, for example trees and shade-tolerant species, such as *Vaccinium myrtillus*, which were also present in the ground flora. *Betula* seeds frequently accounted for a large proportion of the seed bank and seeds of other wind-dispersed species were often present, for example *Cirsium spp.* and *Chamaenerion angustifolium*. The shade-intolerant species with long-lived seeds (eg. *Calluna vulgaris*, *Juncus effusus*, and *Carex spp.*) only occurred at low densities and tended to be more concentrated in the lower soil layers.

Re-coppicing does not always result in ground flora recovery and subsequent seed bank renewal if there has been a long period of neglect, as illustrated by the cut coppice plot at Blanchdown Wood on the Tavistock Woodlands Estate. Seed bank renewal may occur after a period of several years, but this would be limited to the seeds of species still present in the ground flora or those of new species able to colonise the site. The higher seed density in the cut coppice at Yarner Wood, where the period since cutting had been longer, resulted mainly from an increase in the abundance of *Calluna* seeds. The important role of the seed bank in the recolonisation of disturbances has been demonstrated for example in the experimental study of Marks & Mohler (1985) at an old field site and in several studies in tropical forests, for example Young et al. (1987) and Lawton & Putz (1988). In temperate woodlands, the study of Brown & Oosterhuis (1981) illustrates the importance of the seed bank for the survival of shade-intolerant species in coppice woodland. Newly dispersed seed generally plays an insignificant role in recolonisation. In the absence of a seed bank, recovery of the vegetation is often slow and species-poor (Salonen, 1987).

The response of the ground flora to coppicing is limited at acid sites by poor species diversity. At more fertile base-rich sites, a poor response to coppicing may be due to seed bank depletion or to the absence of species from the ground flora. Kirby (1990) measured ground flora changes in an ancient woodland at a base-rich site following coppicing. The increase in species was not as great as that reported in other studies (eg. Ash & Barkham, 1976; Ford & Newbould, 1977). Vernal species were only patchily distributed in the wood. Species such as *Anemone nemorosa* and *Hyacinthoides non-scripta*, are generally absent or poorly-represented in woodland seed banks (see section 8.2.2.). Many other woodland species, such as *Viola riviniana* and *Potentilla sterilis*, have transient seed banks. A response from such species after coppicing or felling can only be expected in areas where they are already present in the ground flora.

Seed bank diversity is retained if trees are felled before depletion has occurred. This is illustrated by the diverse seed bank of the young conifer plantations and felled area at Buckley Wood on the Lindridge Estate, in contrast to the lower species diversity in the seed bank of the abandoned coppice at this site.

Following a study of the Bradford Plan forestry management system by Harris (1986), Harris & Kent (1987a, b) were able to conclude that ground flora diversity is maintained via the presence of different successional stages throughout the forest, in the same way as a traditional coppice system. Such systems, in contrast to clear-felling, should also maintain seed bank diversity.

There were more species present in the seed banks of the B-Plan units at the Tavistock Woodlands Estate than in the neglected coppice at this site. Similar results were reported by Harris (1986). Thus, there is no evidence from this study, or from that of Harris (1986), of seed bank depletion in areas where B-Plan has been introduced.

The time elapsed since the introduction of the system is about 30 years. There are no 30-year-old clear-fell plantations at the site to enable a direct comparison between uneven- and even-aged management systems; in any case this period of time is too short for depletion of the seed banks to have occurred, even in the oldest sub-units. Once the system is fully established, the maintenance of seed bank diversity is dependent on the dispersal of seeds between sub-units (Harris & Kent, 1987b) but this remains to be demonstrated.

Similarly, at the Longleat Estate, although the ground flora beneath the even-aged conifers was depleted in comparison to that beneath the uneven-aged stand, the seed banks were not significantly different. The uneven-aged stand is 18 years old and the plantation 24 years old, which is an insufficient period of time for seed bank depletion to have occurred.

The younger Bradford Plan sub-units and the uneven-aged conifer stand differ in the increased abundance of seeds of species such as *Juncus spp.* and *Agrostis spp.* This is a consequence of the increased abundance of these species in the ground flora.

Changes in management, such as the discontinuation of coppicing or coniferisation, which involves the long-term presence of a canopy will, through the loss of ground flora species due to shading, eventually result in depletion of the seed bank.

8.3.2. Ground Flora

There was an increased abundance of grasses, such as *Agrostis spp.*, *Holcus lanatus* and *Deschampsia flexuosa*, beneath open canopies such as the uneven-aged conifers on the Longleat Estate; following re-coppicing, for example at Blanchdown and Yarner Woods and in cleared areas such as the youngest B-Plan sub-units at Blanchdown and Grenoven Woods. Species which responded to increased light by increasing their cover included *Calluna vulgaris*, for example at Yarner Wood after re-coppicing; *Rubus fruticosus*, for example on the cut coppice at Blanchdown Wood; *Pteridium aquilinum* and *Juncus effusus*, for example in the younger B-Plan sub-units at Blanchdown and Grenoven Woods.

The results of other studies are similar, for example Ash & Barkham (1976) observed that clearings in coppiced woodland in Norfolk were often dominated by species such as *Deschampsia flexuosa*, *Filipendula ulmaria*, *Juncus effusus*, *Pteridium aquilinum* and *Rubus fruticosus*. Similarly, *Deschampsia flexuosa*, *Holcus mollis*, *Rubus fruticosus*, *Pteridium aquilinum* and *Juncus effusus* were amongst the species which became dominant in the clear-felled and heavily thinned areas of woodlands in south east England and the south east Midlands studied by Kirby (1988). Kirby (1990) studied ground flora changes in an ancient woodland in Buckinghamshire, in response to different types of management. *Agrostis stolonifera*, *Deschampsia caespitosa*, *Holcus mollis* and *Juncus spp.* were amongst the species which dominated the ground flora of clear-felled areas. In the coppiced area, *Rubus fruticosus*, rather than grasses, became dominant. Similarly, an increase in cover by existing species, such as *Rubus fruticosus*, rather than invasion by new species, has been reported to occur in gaps created by the removal of trees (eg. Collins & Pickett 1987; McComb & Noble, 1982). The results of these studies suggest that if the amount of disturbance is low, the ground flora species already present increase, but as more disturbance occurs there is a change in species dominance, as grasses and species like *Juncus effusus* become abundant.

The number of species present in the ground flora is influenced by the openness of the canopy. This is determined by a number of factors including stocking density, tree species and management system. For example at the Werrington site fewer species were present in the young spruce plantations, which had been thinned only once or twice than in the older spruce plantation which had been thinned more often and had been damaged by windthrow and spruce aphid infestation. At Buckley Wood, there were more species present in a 20 year-old larch plantation than in a Douglas fir plantation of the same age, since the shade beneath a larch canopy is both less intense and less continuous than that beneath a Douglas fir canopy. At the Longleat Estate, more species were present in the ground flora of uneven-aged than even-aged conifer stands. There were also more species present in the ground flora of the younger B-Plan sub-units than in the older ones. This suggests that uneven-aged forestry management systems do encourage a greater ground flora diversity than even-aged, clear-fell systems.

A reduction in the number of species in the ground flora occurs following neglect, where this is associated with reduced light levels. For example, fewer species were present in the ground flora of the abandoned coppice and oak woodland at Yarner Wood than in the cut coppice; more species were present in the ground flora of managed (well-thinned) than unmanaged oak stands at Blackdog Wood on the Longleat Estate. The number of species present in the cut and uncut coppice at Blanchdown Wood was not different, because of the open canopy of the uncut coppice in the area sampled.

Coniferisation also results in the loss of species from the ground flora. For example, at Buckley Wood there were less species in the ground flora of 20 year-old conifer plantations than in abandoned coppice and fewer in the coppice than in the felled area.

Similar results were obtained by Brown, Pearce & Robertson (1979) in a study of the ground flora of neglected and replanted coppicewoods in south east England and the south west Midlands. More species were recorded under worked than under neglected coppice, and more under coppice than under conifers. The number of species lost as a result of coniferisation was less for larch and pine stands than for Douglas fir and Norway spruce stands. Beech caused a similar reduction to that of the spruce and fir canopies. The influence of tree species on ground flora diversity depends on the intensity of shade beneath the canopy, particularly at the thicket stage. For example Hill & Jones (1978) studied changes in the ground flora in conifer plantations in upland Wales and attributed the reduced abundance of *Pteridium aquilinum* under spruces (*Picea spp.*) and Japanese larch (*Larix leptolepis*) to its elimination at the thicket stage. The species had survived under pines (*Pinus spp.*). Kirby (1988) studied the ground flora of plantations on ancient woodland sites in south east England and the south east Midlands. The decline in species richness and abundance which took place during the thicket stage was less for oak and pine plantations and for some conifer/broadleaf mixtures than for beech, Norway spruce and Lawson cypress.

The number of species present in the ground flora is influenced by the soil type, for example there were more species in the ground flora at the base-rich Buckley Wood site than at the other more acidic sites. On the Longleat Estate, there were also more species in the oak stands on basic soils than in the conifer stands on acidic soils.

Other studies, for example Brown, Pearce & Robertson (1979) and Kirby (1988) have shown that more ground flora species are present on base-rich than base-poor soils and that the reductions in the number of ground flora species due to neglect and coniferisation are less at base-rich sites. The investigation of Staaf et al. (1987) also revealed a trend for an increase in the number of species in the ground flora and seed bank at more fertile sites.

Thus the ground flora and seed bank diversity beneath uneven-aged canopies is greater than that beneath even-aged canopies. However, some (acid) sites do not have the potential to develop a rich ground flora. At the fertile (basic) sites in the lowlands where these systems could be introduced, the potential does exist for a rich ground flora to develop. However, on former agricultural sites the seed bank would be dominated by weeds.

Following the establishment of uneven-aged forestry on sites which were formerly woodland, the flora which is liable to develop will resemble a woodland flora but differ from that present originally. Shade-tolerant woodland species can sometimes survive in the ground flora of abandoned coppice and coniferised woodlands. For example, at Buckley wood, *Mercurialis perennis* and *Arum maculatum* are present in the ground flora of both the abandoned coppice and larch plantation. Vernal species may also survive in abandoned coppice but are generally lost from the ground flora of coniferised woodlands. This is illustrated by the presence of *Anemone nemorosa*, *Hyacinthoides non-scripta* and *Primula vulgaris* in the ground flora of the abandoned coppice at Buckley Wood, but the absence of these species from the larch plantation. Very few species survive in the ground flora of the Douglas fir plantation at this site.

Hill & Jones (1978) compared the ground flora in 30-year old conifer plantations following the afforestation of rough grazings and deciduous woodland in upland Wales. Woodland herbs such as *Oxalis acetosella* and *Hyacinthoides non-scripta* were only present at former woodland sites and had only survived under pine (*Pinus spp.*) and larch (*Larix leptolepis*) canopies and not under spruce (*Picea spp.*). At the Werrington Park Estate, both *Oxalis acetosella* and *Hyacinthoides non-scripta* survive in the ground flora beneath the open canopies of the larch and old spruce plantations.

These shade-tolerant and vernal species can sometimes survive outside woodlands. For example, *Oxalis acetosella* is found in ancient woodland in south east England, but not in recent woodland or in other habitats. In the north and west it occurs in moist or shaded habitats outside woodland (Packham, 1978). Similarly, in the damp and mild climate of western Britain, *Hyacinthoides non-scripta* can be found growing outside woodland, for example on cliff-tops, whereas in the drier south-east it is virtually confined to ancient woodland. These woodland species lack the ability to survive in the seed bank and generally have poor colonising ability. If they are lost from the ground flora of woodlands they are slow to recolonise.

8.4. DIFFICULTIES OF SAMPLING WOODLAND SEED BANKS AND DEVELOPMENT OF IMPROVED SAMPLING TECHNIQUES

The distribution of seeds in the soil is patchy. In the pilot study data, between sample variability in numbers of seeds was high, even for commonly occurring species. Since this may have been attributable to the simple sampling techniques used in the pilot study, a more refined sampling method was developed for the main survey (phase I and phase II sampling). A sampling tool was used to collect the samples to ensure uniformity of sample size. The sampling positions within each 6 m x 6 m square of the sampling plots were randomised, to avoid the possible bias of non-random samples. Sample size was decreased and sample number increased so that the area from which samples were collected was greater. In order to reduce the number of samples in the germination tests, samples were bulked. To assess whether these modifications were successful in reducing between sample variability, between sample variability in the pilot study was compared with that in the phase I samples. Since germination from the phase I samples from the Tavistock Woodlands Estate was poor and insufficient data were available from the phase II samples, the Werrington Park Estate phase I sampling data were used for the comparison. The Tavistock and Werrington sites are similar in terms of soil properties and species present in the seed banks.

The distribution of the number of seeds per sample for the three most common species (*Rubus fruticosus*, *Digitalis purpurea* and *Juncus effusus*) is shown as histograms in Figures 8.1., 8.2. and 8.3. For the pilot study (Figure 8.1.), all three species show a positively skewed distribution. For the phase I sampling from the two young

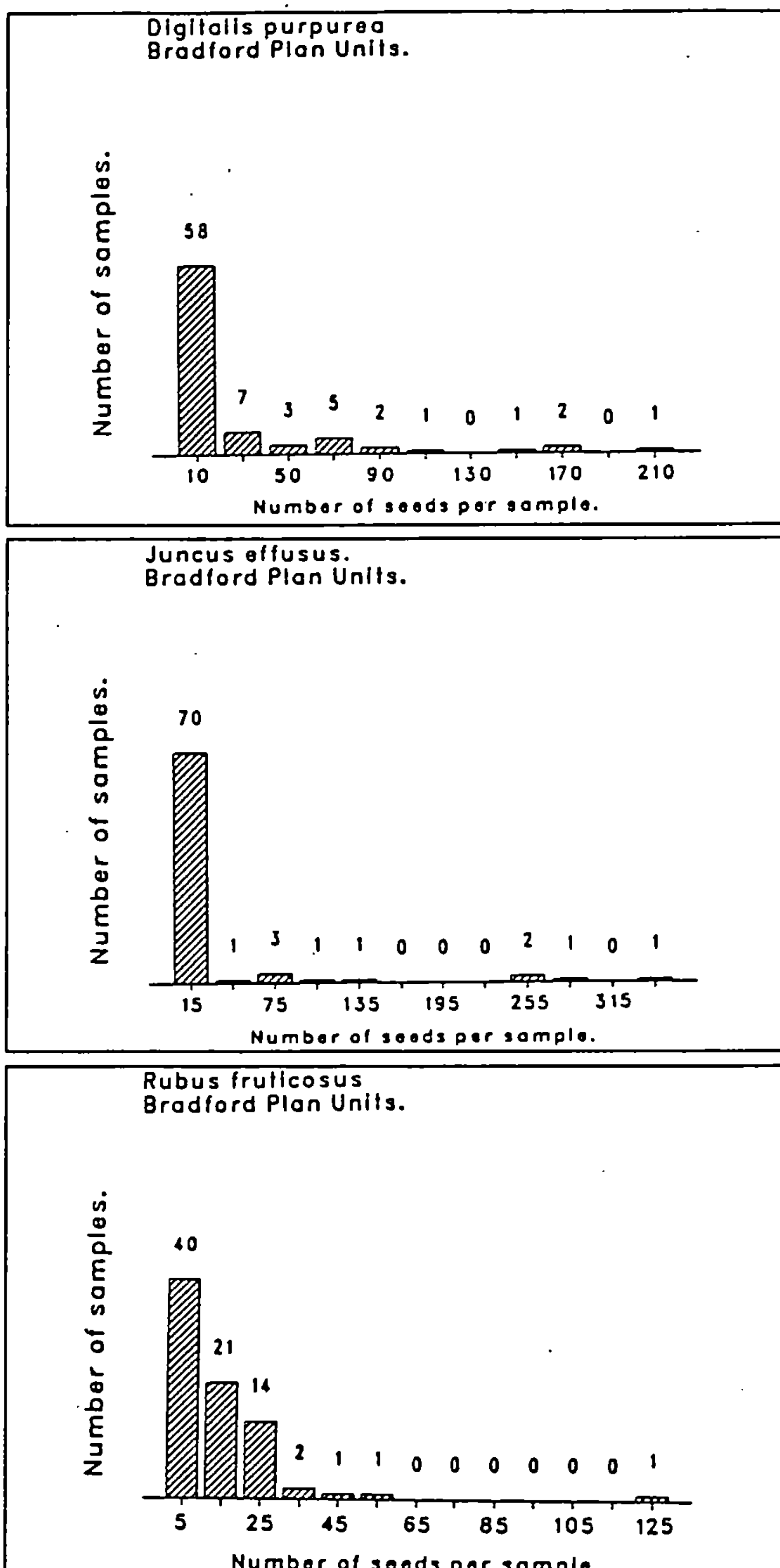


Figure 8.1. Pilot study: Distribution of seeds per sample for the three most common species in the seed bank of the Bradford Plan units at Carthamartha Wood.

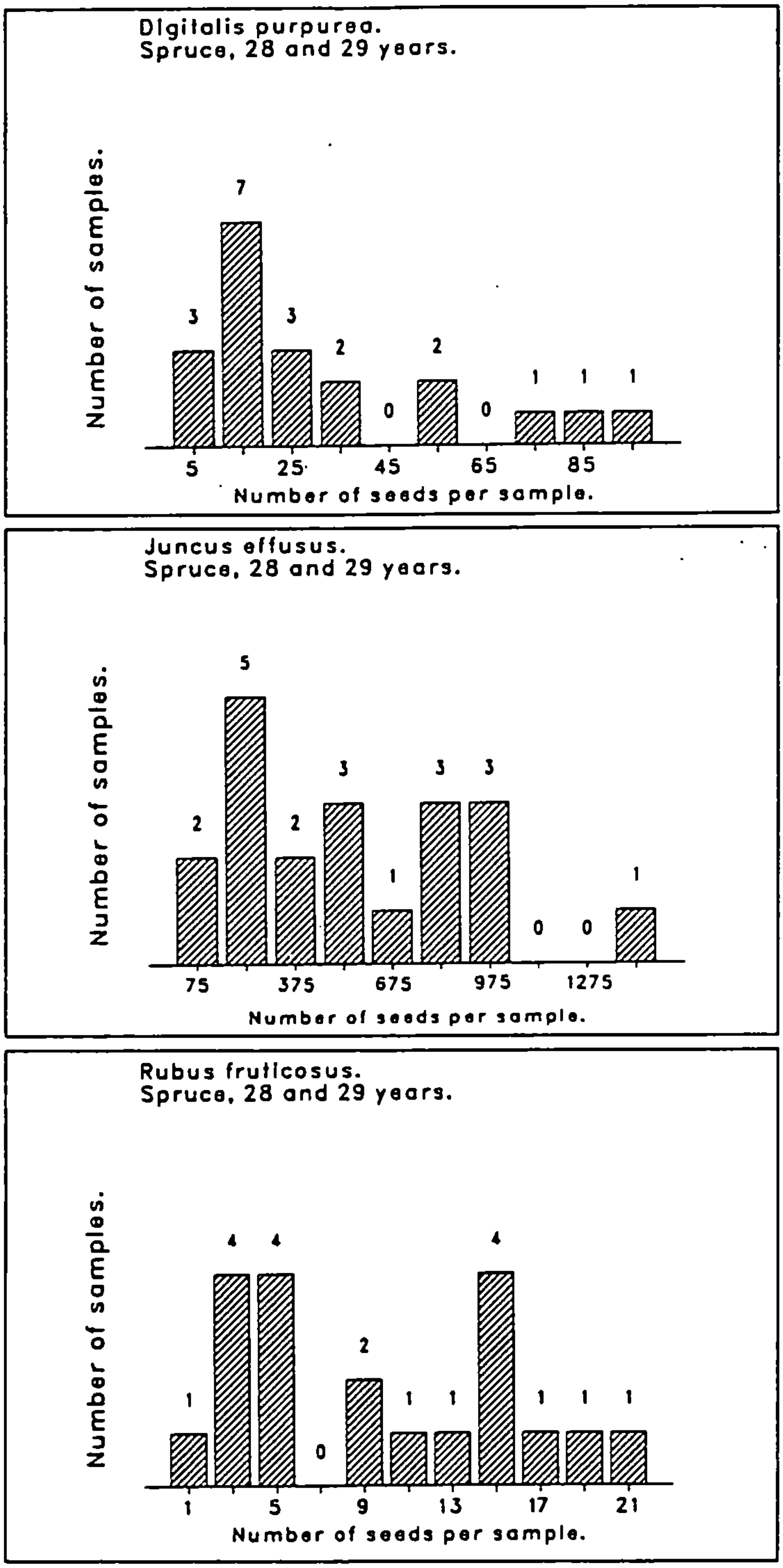


Figure 8.2. Phase I sampling: Distribution of seeds per sample for the three most common species in the seed bank of the two young conifer plantations at the Werrington Park Estate.

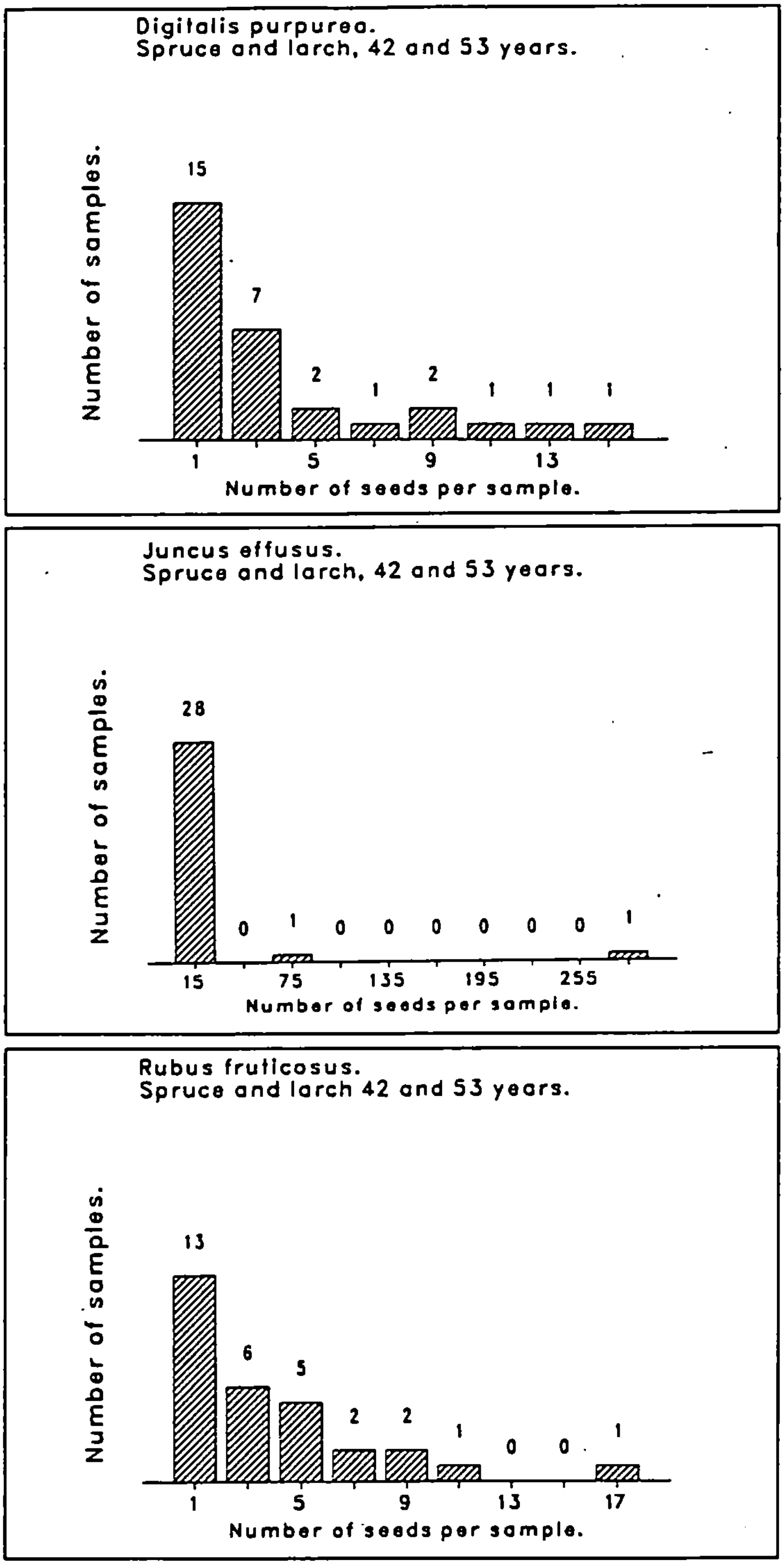


Figure 8.3. Phase I sampling: Distribution of seeds per sample for the three most common species in the seed bank of the three older conifer plantations at the Werrington Park Estate.

plantations (Figure 8.2.) the data are much less skewed, although from the three older plantations (Figure 8.3.) the data are also skewed. The skewness is caused by a large number of samples which have no seeds and a few with many seeds. A more even distribution of seeds in the samples results in a less skewed distribution. This is achieved in the phase I samples from the young plantations but not in those from the older plantations. This is due to the much lower seed densities present in the older plantations. Further increase in the number of samples would be required to sample species occurring at such low densities satisfactorily. However, as discussed in section 2.3., a compromise is necessary between statistical and practical requirements.

The methods of germination testing adopted in this study have a major disadvantage in that the results of the tests take a long time to collect. One year was considered to be the maximum possible time for which samples could be kept in this three year study, although ideally they should have been kept for two or more years. For the latest collected samples, it was only possible to record germination over a six month period. However, seed densities recorded in these samples were not consistently lower than in those kept for longer. For samples collected in the spring, most germination occurs during the first summer. This shorter recording period was therefore sufficient for the purposes of the study.

In the first year of the project, germination from the phase I samples in the shade tunnel was unsatisfactory. This was apparently caused by inadequate water supply. The measures taken to provide a more suitable germination environment for the phase II samples have already been discussed in section 3.4.

8.5. GUIDELINES FOR ENCOURAGING A MORE DIVERSE GROUND FLORA WITHIN CONIFEROUS WOODLAND

The key to good conservation practice is to maintain and add to the range of habitats within the wood (Forestry Commission, 1990). Since the ecological requirements of ground flora species vary, a wide range of habitats increases the potential for retaining a diverse ground flora.

Few woodlands are now worked for the economic production of coppice wood. Worked coppice is of particular conservation value because the system ensures a diverse habitat within the woodland or forest at any one time. Market-orientated coppicing only survives in a few places in south east England, although the system was once used throughout Britain (Rackham, 1980; Peterken, 1981). The case for retaining coppicing as a small but significant component of British woodland management has been reviewed by Peterken (1991).

The uneven-aged forestry systems investigated in this thesis can be thought of as a modern equivalent of the traditional coppice system in that they allow a diverse ground flora and seed bank to be maintained within commercially managed woodland. These systems are particularly appropriate for use in lowland Britain, for example on surplus agricultural land, where soils are more fertile and the climate more favourable than in upland regions.

In conifer plantations, the onset of the inimical thicket stage can be delayed by planting at a wide spacing. The duration of this stage can be shortened by early thinning. A long rotation and low stocking levels, achieved by regular thinning, permit more abundant ground flora development as the stand matures.

Intensive site preparation should be avoided since this can destroy the existing vegetation. This is particularly relevant on ancient woodland sites which may still retain ground flora species of high conservation value.

Site amelioration, such as drainage, weeding and the application of fertilizers, should be planned to minimise adverse affects on the ground flora.

The species associated with rides and open areas are an important component of the woodland ground flora. The creation and maintenance of rides and glades offers opportunities for increasing the diversity of the flora within the wood. The seed banks of rides can provide a reserve of seeds which may be important for the survival of species if seed bank depletion beneath the canopy has occurred.

Broadleaves, with the possible exceptions of beech and hornbeam, which cast dense shade, should be introduced or increased where appropriate. The range of conifer species should be widened, to include those with less dense foliage, particularly the deciduous larches.

The transition from an even to an uneven age structure can be brought about by the use of small felling coupes. If there is some early felling and some delayed felling, a more diverse age structure is eventually obtained. Phased restocking of windthrown areas also increases canopy diversity. Natural regeneration should be used for restocking if possible, since stands developed from natural regeneration tend to be more diverse than planted stands.

8.6. AREAS REQUIRING FURTHER STUDY

8.6.1. Further Seed Bank and Ground Flora Surveys in Woodlands

The surveys described in this thesis were carried out only at a limited number of sites. This was partly due to constraints of time, labour and limited financial resources for travelling. In addition, little previous research has been focused on the seed banks and ground flora of lowland woods, particularly at base-rich sites. All the sites studied were in south west England. Further studies could extend the work, by comparing woodlands in different regions of Britain, and by studying more stands managed using selection systems, including sites in France.

8.6.2. Seed Longevity

The experimental work described in chapter seven focused on interactions between seeds and potential seed-decomposing fungi. The fungal toxicity tests were relatively straight-forward to set up in the laboratory. However, the results of such artificial testing may not be relevant to natural conditions. Further investigations are required before any definite statements can be made concerning the role of seed coat anti-fungal agents in seed longevity in woodland soils.

Experiments investigating other causes of seed loss such as germination, and predation, would be possible topics for further work, as well a more detailed study of seed-decomposing soil fungi and microorganisms.

Earthworms ingest seeds. McRill & Sagar (1973) studied the germination of seeds from worm-casts and found that some seeds pass through the gut without losing viability but that others are destroyed. Worms are selective about which species they ingest (Grant, 1983). Experiments on seed-selection and effects of ingestion on seed viability, using species of worms known to be present in woodlands, would be an interesting topic for investigation.

Further work is needed to investigate the effect of pH on seed longevity. Some studies have recorded the numbers of seeds present in woodland soils of different pH, but the species present at acid and basic sites differ and this makes comparisons difficult. Experimental evidence is required to show whether the longevity of the same species differ in soils of different pH.

8.6.3. Seed Dispersal

No experimental work was carried out to investigate seed dispersal. The use of fluorescent paint to mark seeds and greased seed traps such as those used by Darby (1987), might be techniques worth considering for seed dispersal studies.

Species which would become extinct under the closed canopy of even-aged forests can only survive beneath uneven-aged canopies if they can disperse seed to different parts of the forest. For most British species, there is little information on dispersal mechanisms and distances.

Hodgson & Grime (1990) have discussed various seed dispersal mechanisms and the relevance of seed dispersal and seed banks to vegetation dynamics in various habitats, including woodland. This work could be extended, specifically with reference to woodland species.

8.6.4. Seed Rain

The seed rain survey was not extensive and was only carried out over a six month period. Since seed inputs vary seasonally and annually, they need to be measured over a period of years. The similarity in species composition of the seed rain and seed bank is an interesting result which could be investigated further.

Kellman (1974) monitored the seed rain in two Canadian forest communities over a three year period by trapping seed arriving on the stand floor. Species composition of the seed rain was more similar to the vegetation than the seed bank. Further studies comparing the species composition of the seed rain and seed bank in woodlands are required.

For the seed rain survey, containers were filled with sterile compost and sunk into the ground. The drawbacks of this method of measuring the seed rain have been discussed in section 5.4. An alternative method is the use of greased traps, similar to those used in seed dispersal studies, as described by Wagner (1965). However, these trap only wind-dispersed seeds; seeds dispersed by mammals or insects are not detected.

8.6.5. Vegetative Colonisation

In addition to seed production, many woodland species rely on vegetative expansion in order to maintain or increase their population sizes, for example *Mercurialis perennis* and *Rubus fruticosus*.

Few studies have investigated the relative importance of seed rain, buried seed and vegetative expansion in the colonisation of disturbed sites. An example of such a study is that carried out by Marks & Mohler (1985) at an old field site, which demonstrated that buried seeds and vegetative fragments both played an important role in the early stages of succession. The role of wind-dispersed seed in recolonisation was found to be remarkably insignificant. No similar study has been carried out in temperate woodland.

8.7. CONCLUSION

The primary aim of the thesis, to study the seed banks and ground flora associated with different woodland types in south west England, has been achieved. One of the major problems of studying woodlands is the need for long-term study to assess the effects of changes in management. Within the limitations of a three-year project, much has been learnt about woodland seed banks and ground flora. Inevitably, research projects raise new questions and a number of areas where further study is required have been identified. The work has highlighted the potential for future seed bank and ground flora research and as a result may serve to draw attention to a promising field for further inquiry.

With current changing attitudes, forestry practices which maximise timber production at the expense of nature conservation are becoming increasing unacceptable. The uneven-aged forestry systems described in this thesis allow an alternative conservation-conscious approach to commercial forestry. With the financial incentives available for encouraging the expansion of forestry in the British lowlands, these systems could be much more widely used in the future.

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